FINE-SCALE MOVEMENTS AND HABITAT USE OF THE SOUTHERN GROUND-HORNBILL *BUCORVUS LEADBEATERI*

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Dissertation presented for the degree of Master of Science

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May 2015

Plagiarism declaration

I understand and appreciate the meaning of plagiarism and declare that all the work in the dissertation, save for which is properly acknowledged, is my own.

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Table of contents

Abstract

Southern Ground-Hornbills *Bucorvus leadbeateri* are listed as Endangered in South Africa and there is a concerted effort to reverse their population decline. Understanding the factors affecting their movement patterns and how they interact with their habitat is useful to inform conservation and habitat management options for the species, to select sites for artificial nests and to identify suitable areas for reintroduction initiatives. In this study, I report daily and seasonal patterns of habitat use as well as patterns of roost site use of four Southern Ground-Hornbill groups in the Associated Private Nature Reserves, northeast South Africa, based on data from GPS-satellite tags collected over one year from October 2010 to September 2011. Home ranges varied from 5.9-10.3 km^2 and were larger in winter than during the summer breeding season. Daily travel distances were greater during the breeding season, when birds were constrained to forage close to their nest, and were lower in winter, when birds ranged more widely. Hourly travel distances were affected by time of day, season, air temperature and group. Birds travelled farthest per hour in the morning, decreasing in the afternoon in winter. However, in summer hourly travel distances were bimodally distributed, with a minimum during the middle of the day when ambient temperatures exceed 25˚C. Acacia-dominated vegetation and riparian habitats were favoured disproportionately during the heat of the day in summer, presumably because they offer more shade than other habitats. The number of roost sites used per month decreased progressively throughout the Early Wet season (October-December) and was lowest during the Late Wet season (January–March) for three groups that bred successfully. Mean monthly nights per roost were highest for these groups in the Early Wet and Late Wet seasons, specifically over December and January, coinciding with the peak breeding period. Throughout the Early Wet season, all four groups frequently roosted in close proximity to the nest, with 54–83% of roosts being within 1 000 m of the nest. During the Wet season, riparian habitats were favoured for roosting by the three groups that bred successfully, while during the dry season, disturbed areas, combretum-dominated habitats and mopane-dominated habitats were used. I conclude that the optimal habitat configurations for ground-hornbills include a mosaic of habitat types, including open areas for foraging and dense trees for shade as well as adequate large trees for nesting and roosting, particularly in riparian habitats.

Acknowledgements

First and foremost, I would like to thank Dr Rob Little and Prof. Peter Ryan for their guidance and assistance throughout the course of this project. Their experience, expertise and enthusiasm were invaluable and without their help, this project would not have been possible. I specifically thank them for their patience in dealing with my challenges along the way. Your insight and support is truly appreciated.

I would also like to thank Kate Carstens for her input, friendship and continued support throughout the completion of this project. I particularly enjoyed the time we spent together in the field.

I am also grateful to Nicholas Lindenberg and Thomas Slingsby for their expert GIS advice as well as Tim Reid for his assistance with the statistical analysis and modelling.

Special thanks to Hilary Buchanan and Chris Tobler for their administrative support and help whilst on campus.

Thank you to the DST-NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology for the funding provided for this project.

On a personal level, I would like to thank my family and friends, especially my father Anthony Zoghby, who constantly believed in me and supported me until the very end and my girlfriend Sarah Allderman for the incredible line drawings.

Finally, a special thanks to the late Prof. Phil Hockey for giving me the opportunity to take on this project and for the initial input and guidance. My only regret is that he is not able to see the completed work.

CHAPTER 1

GENERAL INTRODUCTION

The use of animal tracking and the invaluable information that it generates, allows wildlife managers to effectively achieve their primary goals. These include the application of scientific information and technical skills to safeguard, protect and conserve wildlife and its habitats (Thomas *et al.,* 2008; Thomas *et al.,* 2010). This thesis uses GPS locational data collected by animal tracking to describe the fine-scale movements and habitat use of the endangered Southern Ground-Hornbill *Bucorvus leadbeateri* to better understand how the species interacts with its habitat and to help inform future conservation and management decisions.

Overview of the concepts of habitat and habitat use

An animal's habitat is fundamentally important for its survival and reproductive success, since it provides the animal with the necessary resources for fulfilling its life-history requirements (Block & Brennan, 1993; Krausman, 1999; Beyer *et al.,* 2010). Equally important, is how an animal utilises and interacts with its preferred habitats. In terms of wildlife management, understanding a species' preferred habitats and habitat ecology is of paramount importance for facilitating informative conservation and management decisions (Beck *et al*., 2001; Morrison *et al.,* 2005; Groom *et al.,* 2005).

A habitat is a region in environmental space defined by the sum of environmental resources, both physical and biological, that influence the location of an animal (Krausman, 1999; Beyer *et al.,* 2010). Resources such as food, shelter, water and special factors needed for survival and reproductive success influence the location of an animal directly (e.g. forage quality) or indirectly (e.g. altitude; Block & Brennan, 1993; Krausman, 1999; Beyer *et al.,* 2010). Habitat generally provides the necessary resources that an animal needs to survive and includes migration and dispersal corridors as well as areas that are occupied during both the breeding and nonbreeding seasons (Krausman, 1999). Preferred habitats therefore imply more than just vegetation or vegetation structure (Krausman, 1999).

Habitat use is the manner in which an animal utilises the environmental resources within its choice of habitats (Block & Brennan, 1993; Krausman, 1999). Environmental resources are usually distributed heterogeneously in space and time and therefore require spatial and temporal adjustments by an animal, resulting in a continuum of differential space use within a given habitat type (Block & Brennan, 1993; Beyer *et al.,* 2010; Kie *et al.,* 2010). Different habitats may be used for various aspects of an animal's life, such as for foraging, cover, breeding and roosting. The categories of habitat use may divide habitat, but overlap in areas of use often occur, e.g. an area used for foraging may have the same physical characteristics as an area used for cover (Krausman, 1999). The area traversed by an animal in its normal activities of foraging, mating and caring for young is known as the animals' home range (Burt, 1943). Home ranges are not constant, as animals vary their activities in definite areas across time, and even within their home range, a matrix of varying intensity use exists (Odum & Kuenzler, 1955). Home range size is dependent on a broad scale of factors including, but not limited to, diet, metabolic needs, body weight, food availability, energy expenditure, habitat qualities such as access to water and refugia, seasonality, and social factors such as group size, population density and competition (Bertram, 1973; Harestad & Bunell, 1979; Gittleman & Harvey, 1982; MacDonald, 1983; van Orsdol *et al.*, 1985; Spong, 2002). The home range of an animal is often shared with conspecifics, resulting in overlap between individuals or groups (Burt, 1943; Odum & Kuenzler, 1955). If however the home range or parts of the home range are actively defended against conspecifics, that particular area is termed a territory (Burt, 1943). The establishment of home ranges and territories produces a characteristic intra-population distribution of space-use (Odum & Kuenzler, 1955).

Preferred habitats are selected by an animal based on a hierarchical process involving a series of innate and learned behavioural decisions about what habitats to use at different scales of the environment (Krausman, 1999). Several interacting factors often influence habitat selection, with the outcome usually being a trade-off between those best suited to the animal and those available at that point in time (Krausman, 1999). For terrestrial animals, factors include, among others, forage quality and quantity, access to water, cover, inter- and intra-specific competition, the risk of predation, and the availability of resting, roosting and breeding sites (Block & Brennan, 1993; Krausman, 1999). Habitat preference is the outcome of habitat selection and is the non-random and disproportionate use of particular habitats in an environment (Block & Brennan, 1993; Krausman, 1999; Beyer *et al.,* 2010).

By combining the knowledge of animal movement and distribution data with *in situ* measurements of habitat characteristics, meaningful interpretations of habitat use and preferences can be derived (Beyer *et al*., 2010; Hebblewhite & Haydon, 2010). Quantifying and analysing differential space use within heterogeneous habitats can provide conservation managers with greater insight into the preferred habitats of a species and the ecological processes that give rise to spatial patterns of habitat use (Krausman, 1999; Beyer *et al.,* 2010). Understanding the interaction between an animal and its preferred habitats has been made easier by the use of advanced telemetry and Global Positioning System (GPS)-based animal tracking.

Introduction to animal tracking and its role in wildlife management

Animal tracking is part of the broader field of telemetry, which is the remote measurement and recording of locational data (Cooke *et al.,* 2004; Ponganis *et al.,* 2007). Although the field is still relatively young, it has provided a major breakthrough in wildlife studies, allowing for an efficient and accurate means of acquiring spatio-temporal data of animal movements which is a vast improvement on previous, mostly labour-intensive direct observation methods (Johnson *et al.,* 2000; Mourao & Medri, 2002; Adrados *et al.,* 2003; Ungar *et al.,* 2005). Most tracking approaches involve attaching a transmitter and/or receiver to an animal to record its position over time, calculating coordinates by measuring the change in frequency (Doppler shift) of signals sent from an array of 24 earth-orbiting GPS satellites received by the animal-born device (Cooke *et al.,* 2004; Johnson & Ganskopp, 2008). The coordinates are then stored in onboard memory (data loggers) or transmitted, e.g. to satellites or via cell phone networks from where they can be downloaded at regular intervals (Cooke *et al.,* 2004). This information, coupled with the advances in analytical tools used for interpreting patterns of spatio-temporal data, have made it possible to conduct detailed home range analyses of animals and to investigate their movements and patterns of habitat use within a region (Cooke *et al.,* 2004; Kie *et al.,* 2010). Understanding these and other facets of a species' habitat ecology have made it possible to introduce more adaptive conservation management plans and policies for particular species (Beyer *et al*., 2010; Hebblewhite & Haydon, 2010).

The ecological insight gained from studies making use of animal tracking have already helped inform conservation decisions on a suite of species, ranging from small birds, such as Northern Wheatears (*Oenanthe oenanthe* – Schmaljohann *et al.,* 2012) to large terrestrial mammals such as the African Elephant (*Loxodonta africana* – Thomas *et al.,* 2008) and include marine species such as the Whale Shark (*Rhincodon typus* – Eckert & Stewart, 2000) and dangerous and aggressive species such as the Estuarine Crocodile (*Crocodylus porosus* – Kay, 2004).

Biology and ecology of the Southern Ground-Hornbill

The Southern Ground-Hornbill *Bucorvus leadbeateri*, currently listed as globally Vulnerable to extinction (BirdLife International, 2014) and regionally Endangered (Taylor *et al.,* 2015), is one of two species in the family Bucorvidae - the other being the Northern Ground-Hornbill *B. abyissincus.* The Bucorvidae are most notably separated from true hornbills (Bucerotidae) by not sealing the female into the nest cavity while breeding (Kemp, 1995). The two species are allopatric in African savannas and grasslands on either side of the equator (Kemp, 1995).

Southern Ground-Hornbills occur in suitable habitat in South Africa, Botswana, Namibia, Mozambique, Zimbabwe, Angola, Zambia, Malawi, Democratic Republic of Congo, Tanzania and Kenya (Kemp, 1995). In South Africa, they occur most commonly in Limpopo, Mpumalanga, KwaZulu-Natal and the Eastern Cape Province, but also have been recorded in Gauteng and the Free State (Kemp & Webster, 2008). The highest recorded density is at Mana Pools, Zimbabwe (one group every 20 km^2), while in South Africa, densities are much lower (one group per 100 km^2) (Kemp & Kemp, 1980; Barnes, 2000; Hockey *et al.,* 2005).

Adults have a body length of 90-130 cm and weigh 2.5-6 kg (Hockey *et al.*, 2005). Both sexes have black plumage, with white primaries and primary coverts and extensive bare facial and inflatable throat skin (red in males and red with a violet-blue patch under the throat in females) (Kemp, 1995; Hockey *et al.*, 2005). They are the largest co-operatively breeding bird in the world, living in social groups comprising 2-12 members (mostly 3-5 members; Kemp, 1995). Groups consist of an alpha breeding pair assisted by ≤5 adult males and ≤4 immature individuals of either sex (Hockey *et al.,* 2005). Non-breeding group members are generally retained offspring of the dominant pair (Kemp, 1995). These individuals are subordinate helpers who contribute to group activities, including food provisioning to the incubating alpha female and growing chick (Kemp, 1995).

Southern Ground-Hornbills occupy year-round home ranges, which they actively defend (Kemp *et al.*, 1989). Territory defence is undertaken by adult group members and consists of regular pre-dawn vocalisations while still at the roost site and high aerial pursuits if groups hear or encounter rival neighbours (Kemp & Kemp, 1980). Their deep booming call, which is audible to humans at distances of up to 5 km, is most often a duet initiated by the alpha breeding pair, with the male calling at a lower pitch than the female (Kemp, 1995).

Ground-hornbills nest in natural cavities in trees and occasionally in rock or earth-bank cavities, requiring an internal cavity diameter ≥40 cm (Kemp & Kemp, 1980; Msimanga, 2004). This demands relatively large trees, which in drier habitats generally occur along watercourses. Tree species likely to form trunks/branches with cavities of sufficient size, and that are used most often in South Africa, include *Ficus sycomorus* and *Diosypros mespiliformis* along watercourses and *Sclerocarya birrea* and *Adansonia digitata* away from drainage lines (Kemp & Begg, 1996; Jordan, 2011). *Combretum imberbe*, a tree species with exceptionally hard wood that occurs both along and away from watercourses, is also frequently used for nesting (Kemp & Begg, 1996). Once a suitable nest site has been selected, the alpha female spends approximately five hours a day in the cavity, preparing the inside of the nest. During this time, the alpha male and the helpers bring dried leaves and food items for the alpha female (Kemp & Kemp, 1980).

The onset of breeding behaviour is governed by food availability and is usually prompted by the first heavy summer rains, with egg-laying typically between August and January, peaking in October-November (Kemp & Kemp, 1991). Clutch size is small, 1-2 (rarely 3) eggs, laid 3-5 days apart, and incubation starts once the first egg is laid (Kemp, 1976; Kemp & Kemp, 1991). Only the alpha female incubates the eggs and broods the chicks, being fed at the nest by the alpha male and, to a lesser extent, by the helpers. After an incubation period of roughly 42 days, the eggs hatch and the female begins feeding the chicks whole food items (Kemp 1976; Kemp, 1991). Generally, only one chick fledges per season. If two eggs hatch, the second chick dies after a few days from dehydration and starvation due to parental neglect and competition with its older and thus larger sibling (Kemp & Kemp, 1980).

At fledging, after a nestling period of around 86 days, the chick leaves the nest and does not return (Kemp & Kemp, 1991). For the first year, the chick is accompanied constantly by a sub-adult and remains with, and is fed by, members of the group (Kemp, 1976; Kemp & Kemp, 1991). Thereafter, juveniles remain with the parental group for several years, exhibiting a prolonged post-fledging dependency and delayed maturity (estimated age of 5-6 years for both males and females, with breeding attempts only occurring much later) (Kemp & Kemp, 1980; Kemp, 1995; Morrison *et al.,* 2005). Upon reaching maturity and after having obtained their full facial colouring, females tend to disperse from their natal group in search of another group or to start a new group themselves, with the first breeding attempts estimated to occur after birds are at least nine years old in South Africa (Kemp, 1976; Kemp & Kemp, 1991; Kemp, 1995).

Southern Ground-Hornbills typically have a slow reproductive output, with groups in the Kruger National Park (KNP) fledging one chick in 49% of breeding attempts, and only 31% of fledged chicks surviving to maturity (Hockey *et al.*, 2005). Groups do not breed every year, and on average, only fledge one chick every 9.3 years (n = 215 group breeding seasons) (Kemp, 1988). Studies in the Associated Private Nature Reserves (APNR), adjacent to the KNP, have revealed social and environmental factors that influence the breeding performance of Southern Ground-Hornbills, with results showing considerable inter-group variation in the frequency and success of breeding (Wilson & Hockey, 2013). During eight breeding seasons between 2001 and 2009, some groups bred and successfully fledged a chick every year, while others did not rear a single chick. Of 67 breeding attempts monitored, 51 (76%) were successful, with seven of the groups (30%) collectively contributing 60% of chick production. Total rainfall over the breeding season, nest type (natural versus artificial), the interaction of nest type with the proportion of open woodland within 3 km of the nest site, and group size all affected breeding performance (Wilson & Hockey, 2013).

Conservation of Southern Ground-Hornbills in South Africa

In South Africa, the Southern Ground-Hornbill has experienced a 65% reduction in their range and numbers over the past century, with an estimated population of only 1 500 individuals remaining nationally, most of which are in protected areas (Hockey *et* al., 2005; Kemp & Webster, 2008). The decline in numbers can be largely attributed to human causes, with the primary reason being the loss and fragmentation of suitable habitat (Vernon, 1986). In addition, bush encroachment, brought on by increased grazing pressure of herbivores, soil erosion, changes in fire regimes and increases in CO_2 concentrations have reduced the biodiversity and productivity of landscapes, adversely affecting the foraging efficiency of groups (Vernon, 1986; Barnes, 2000; del Hoyo *et al*, 2001; BirdLife International, 2014). Direct factors, such as electrocution, poisoning, trade in live birds, use in traditional practises, and persecution for window breaking have also contributed to population declines and local extinction (Kemp & Webster, 2008; Coetzee, 2014).

The rapid decrease in the population of this long-lived, slow reproducing species is cause for concern, and as such, the species has become the focus of several conservation and management efforts (Hockey *et al.,* 2005; Morrison *et al.,* 2005; Jordan, 2011). Over the last two decades, these have included research studies, education and awareness campaigns, harvesting and hand rearing of second-hatched chicks, captive breeding programmes, reintroductions into former parts of the species' historical range, and the erection of artificial nests (Morrison *et al.,* 2005; Jordan, 2011; Wilson & Hockey, 2013).

In 2005, the species was subject to a population habitat viability assessment workshop, involving over 30 stakeholders working towards the conservation of Southern Ground-Hornbills in South Africa (Morrison *et al*., 2005). This workshop highlighted the lack of scientific data and the need to further investigate the biology and ecology of the species to focus and improve conservation and management decisions (Morrison *et al*., 2005). A key recommendation was designing a capture technique, which made the fitting of transmitters for animal tracking and the collection of morphometric and genetic data possible (Theron, 2011). Subsequent studies have contributed significantly towards understanding the biology and ecology of the species, however, the recently published Southern Ground-Hornbill Species Recovery Plan for South Africa highlights areas of the species' research and conservation that still require further action (Jordan*,* 2011). Key gaps in existing knowledge include: (a) an analysis of the species' current range, (b) estimates of its population size in South Africa, (c) an evaluation of the species' genetic structure and diversity in Africa, (d) an appraisal of the likely impacts of climate change on the species, (e) a greater understanding of the species' population dynamics with regards to recruitment and dispersal, and (f) an investigation of the habitat requirements of the species (Jordan*,* 2011). This thesis contributes towards understanding the habitat requirements of the Southern Ground-Hornbill, and in turn, adds to the existing knowledge on the biology and ecology of the species.

Objectives and dissertation outline

The objective of this thesis is to investigate the patterns of habitat use of Southern Ground-Hornbills in the Associated Private Nature Reserves (APNR). This was achieved by analysing year-round GPS locational data from four ground-hornbill groups and describing the seasonal changes in habitat use and patterns of roost site use.

The dissertation comprises two substantive chapters, focussed on specific yet interrelated aspects of the species' habitat ecology, followed by a brief synthesis and reference list.

Chapter 2: Seasonal changes in movement and habitat use by Southern Ground-Hornbills in the South African lowveld

Seasonal patterns of habitat use have been described for this species (Dickens, 2010; Wyness 2011; Theron *et al.,* 2013), however daily patterns of habitat use and how daily patterns change seasonally remains largely unstudied. A deeper understanding of how Southern Ground-Hornbills interact with their habitat would help inform conservation and management decisions by assisting in identifying optimal habit configurations for the species. In this chapter I investigate aspects of fine-scale habitat use of the Southern Ground-Hornbill: daily travel distances, diurnal movement patterns and spatial foraging patterns.

Chapter 3: Patterns of roost site selection and use by Southern Ground-Hornbills in the South African lowveld

Existing knowledge on the roosting habits of Southern Ground-Hornbills is limited, with groups said to roost in large trees, apparently where they ended up after daily foraging (Kemp & Kemp, 1980). In this chapter I investigate patterns of roost site use by quantifying the number of roost sites utilised per month, quantifying roost site use frequency, investigating distances between roost sites and the nest, and lastly, assessing roost sites in relation to the vegetation type in which they occur.

CHAPTER 2

SEASONAL CHANGES IN MOVEMENT AND HABITAT USE BY SOUTHERN GROUND-HONRBILLS IN THE SOUTH AFRICAN LOWVELD

Abstract

Southern Ground-Hornbills *Bucorvus leadbeateri* are listed as Endangered in South Africa and there is a concerted effort to reverse their population decline. They live in groups year round, with only the alpha pair breeding, raising at most one chick per year. Each group has a home range of 50–100 km^2, but there are few data of their spatial habitat use within this range. Understanding the factors affecting ground-hornbill movement patterns is useful to assess habitat management options for the species, to select sites for artificial nests and to identify suitable areas for reintroduction initiatives. In this chapter I report daily and seasonal patterns of habitat use by four Southern Ground-Hornbill groups in the Associated Private Nature Reserves, northeast South Africa, based on data from GPS-satellite tags. Daily travel distances averaged 7.4 ± 2.2 $km.day^{-1}$; they were greater during the breeding season, when birds were constrained to forage close to their nest but were required to make repeated visits with food, and were lower in winter, when birds could range more widely. Hourly travel distances were affected by time of day, season, air temperature and group. Birds travelled farthest per hour in the morning, decreasing in the afternoon in winter. However, in summer hourly travel distances were bimodally distributed, with a minimum during the middle of the day when ambient temperatures exceed 25˚C. Acacia-dominated vegetation and riparian habitats were favoured disproportionately during the heat of the day in summer, presumably because they offer more shade than other habitats. Optimal habitat configurations for ground-hornbills include a mosaic of habitat types, including open areas for foraging and dense trees for shade.

Introduction

Understanding a species' pattern of habitat use is central to its effective conservation and management. Such information is limited for the Southern Ground-Hornbill *Bucorvus leadbeateri* (Jordan, 2011), which is considered Endangered in South Africa (Taylor *et al*., 2015) and Vulnerable globally (BirdLife International, 2014) as a result of a decrease in range and population density.

Southern Ground-Hornbills remain in family groups year-round, with home ranges of 50-100 km^2, determined primarily by the availability of suitable nest sites and secondarily by food availability during the dry season (Hockey *et al.,* 2005; Wilson & Hockey, 2013). Throughout their range, ground-hornbills occur in grassland and savannah habitats, favouring open areas where prey is easily detected (Kemp, 2005). They display a degree of seasonal habitat selectivity by favouring different habitat types at different times of the year (Theron, 2011).

When foraging, Southern Ground-Hornbill groups move through the landscape cohesively in search of prey, which includes reptiles, insects, amphibians, small birds and mammals (Kemp & Kemp, 1980; Vernon, 1986). Prey is located while walking slowly in a phalanx formation, searching the ground and surrounding vegetation, picking up or actively pursuing each prey item. In the dry season, they dig in dung heaps of large herbivores, where they find up to 30% of their prey (Hockey *et al.,* 2005).

Activity is often governed by ambient temperature, decreasing towards midday, when groups seek and rest in areas of shade, and increasing again thereafter (Kemp & Kemp, 1980). Southern Ground-Hornbills appear susceptible to overheating, showing the first signs of heat dissipation behaviour (wings raised, upper wing coverts erect, wrists apart, open bill, drooping primaries and watering from the nostrils) at ambient temperatures of 26˚C (Kemp & Kemp, 1980; Kemp, 1995). Once air temperatures exceed this level, ground-hornbills reduce activity and stop to rest in areas of shade at temperatures above 30˚C (Kemp & Kemp, 1980; Kemp, 1995).

This study reports patterns of habitat use by four groups of Southern Ground-Hornbills that were tracked for a year with GPS-satellite transmitters in the South African lowveld. Hourly positional data were used to record spatio-temporal patterns of habitat use and to test daily and seasonal differences in travel distances in relation to ambient temperature and breeding activity. Understanding the factors affecting ground-hornbill movement patterns is useful for assessing habitat management options for the species, selecting sites for artificial nests and for identifying suitable areas for reintroduction initiatives.

Study site

The Associated Private Nature Reserves (APNR) is a complex of privately owned nature reserves in the Limpopo Province, South Africa, collectively representing 180 000 ha dedicated to conservation (van Rooyen *et al.,* 2005; Figure 2.1). The APNR is adjacent to the western boundary of the Kruger National Park (KNP) and forms part of the Greater Kruger National Park Biosphere Reserve along with the Sabi-Sand Game Reserve and other provincial nature reserves (Greyling *et al.,* 2004).

Figure 2.1: The Associated Private Nature Reserves study site in northeast South Africa adjacent to the Kruger National Park (24˚02'S - 24˚33'S and 30˚49'E - 31˚29'E).

The climate is sub-tropical with hot, humid summers and warm, dry winters (Venter *et al.,* 2003). Temperatures range from a mean minimum of 9.4˚C in June, the coldest month, to a mean maximum of 33.6˚C in January, the hottest month (Venter *et al.,* 2003). Mean annual rainfall ranges from 450 mm in the northeast, to 600 mm in the southwest. Rain mainly falls in summer (October-March) and accounts for approximately 90% of the annual total rainfall (van der Waal, 2010).

Soils in the APNR are mainly derived from granite, comprising of shallow sandy loam or gravel, and have a coarse texture and low nutrient availability (Venter *et al.,* 2003; van Rooyen *et al.,* 2005). The landscape is heterogeneous, varying from open savanna to closed woodland, incorporating a mix of lowland savanna, open tree savanna, mixed and open woodland, low thicket and shrubveld (Venter & Gertenbach, 1986; van Rooyen *et al.,* 2005; van der Waal, 2010). This study recognises six broad habitat types: acacia, combretum, mopane and terminalia dominated vegetation as well as riparian and disturbed habitats (Figure 2.2). These are based on the 22 dominant plant species and community compositions defined by van Rooyen *et al.* (2005; Appendix 2.1).

Methods

The study used GPS-satellite transmitters to track four Southern Ground-Hornbill groups, named Kharan Khaya, Keer Keer, Rhino Road and Senelala after localities in their home range. Birds were captured using a walk-in tunnel trap made of game capture netting, which had a curtain that could be pulled across the entrance once birds entered. A decoy Southern Ground-Hornbill model was placed inside the trap and recorded calls were played to attract birds to the trap (Figure 2.3). Once birds entered the trap, the curtain was pulled shut by an observer in a vehicle parked 100 m away. Birds in the trap were then caught for processing and one bird per group was fitted with a solar-powered Argos/GPS PTT-100 transmitter (Microwave Telemetry Inc, Columbia). The devices had solar panels to power long-term data collection (2 years maximum) and weighed 70 g, just over 1% of the mass of an adult Southern Ground-Hornbill (Hockey *et al.,* 2005). Devices were attached with a back-harness system secured around the birds' wings (Figure 2.4) and were programmed to record locations every hour from 04:00 to 00:00.

Because groups forage as a cohesive unit and remain together throughout the day, it is only necessary to track one bird per group (Kemp & Kemp 1980; Kemp, 1995). Subordinate adult males or sub-adults were fitted with a transmitter rather than the alpha pair because of their social importance to the group. Birds were tracked from October 2010 to September 2011, but the device was lost from the Rhino Road group in February 2011 and could only be redeployed in April 2011. All four groups attempted to breed in the 2010 – 2011 breeding season, but the Senelala groups' chick died sometime in November 2011, allowing the group to range more widely than the other groups in the second half of the austral summer.

GPS fixes were decoded using MTI Argos-GPS Parser software, projected in Universal Transverse Mercator 36˚ South (UTM 36S), and overlaid on a geo-referenced vegetation map of the APNR using ArcGIS® 9.3. Movement patterns were analysed using Home Range Tools (HRT) and Hawth's Analysis Tools for ArcGIS® 9.3 (Beyer, 2007).

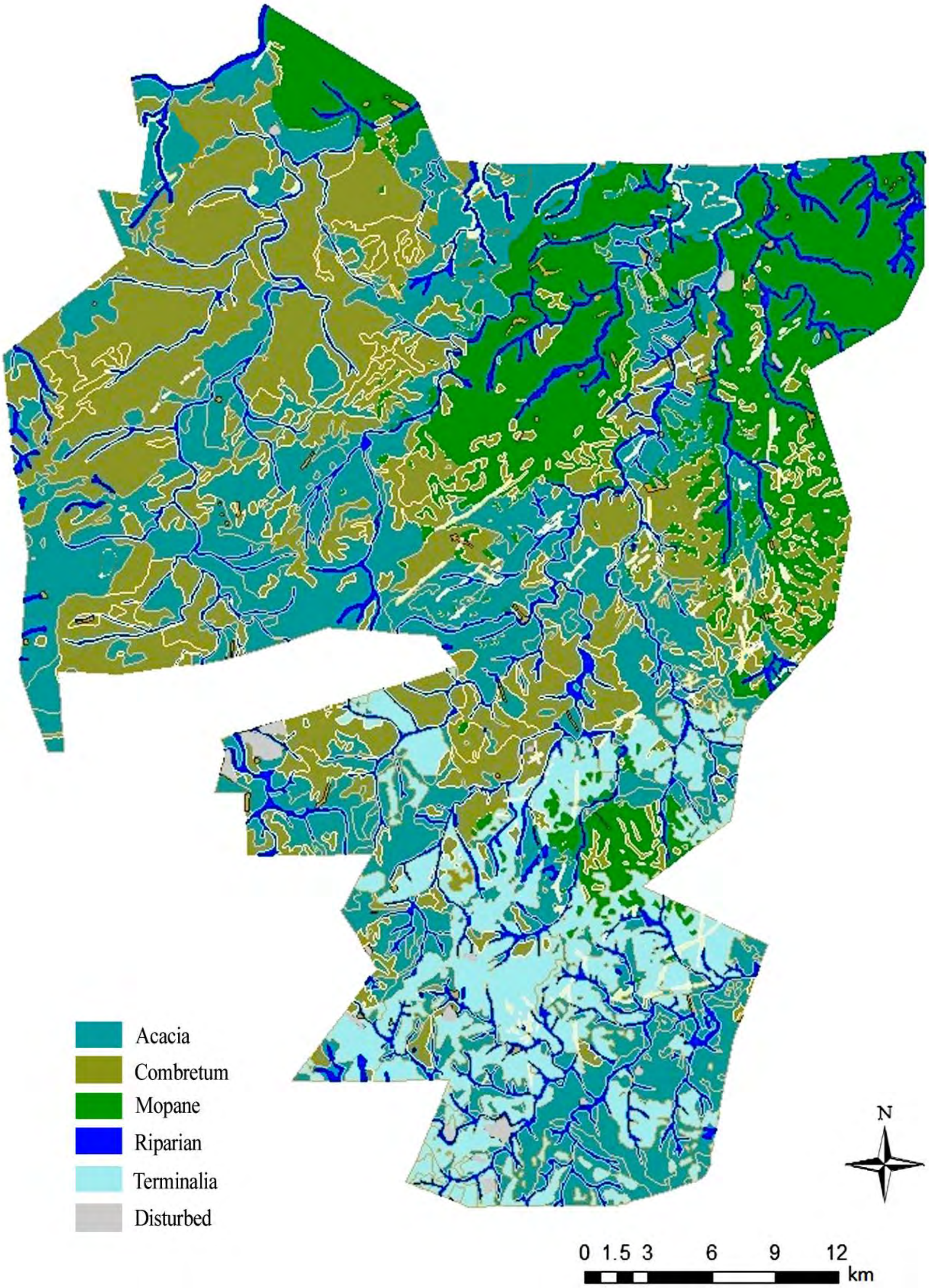


Figure 2.2: The Associated Private Nature Reserves showing broad habitat types.

Figure 2.3: Walk-in tunnel trap showing decoy Southern Ground-Hornbill models and the housing of the tape recorder for play-back calls (Photos Phil Hockey).

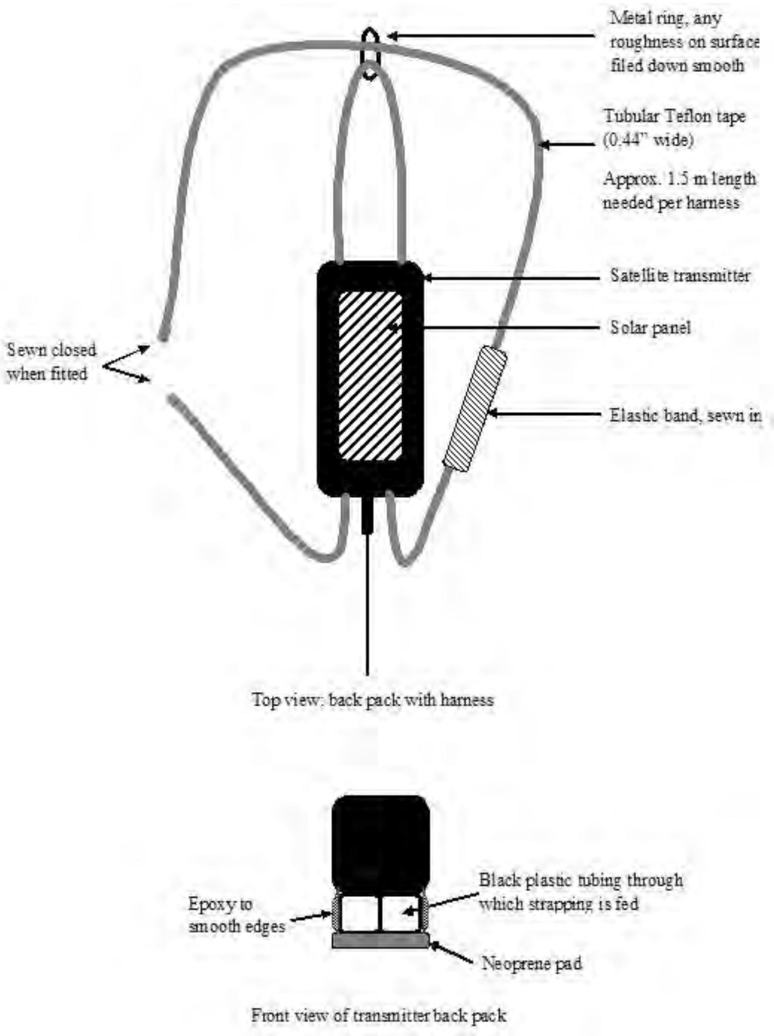


Figure 2.4: Schematic of the tracking device and harness utilised in this study.

Displacement between successive GPS fixes was estimated in ArcGIS® 9.3. Because animal movements are complex, the interval between successive GPS fixes affects estimates of travel distance (Patterson *et al.,* 2008). Dickens (2010) recorded the location of a habituated Southern Ground-Hornbill group in the Mabula Private Game Reserve, northeast South Africa, every 5 minutes to determine the extent of information loss resulting from sampling ground-hornbill locations at different intervals (Figure 2.5). Recording positions hourly underestimated travel distances by ~38% compared to records every 5 minutes, so all travel distances were extrapolated by this factor (1.38 x observed values).

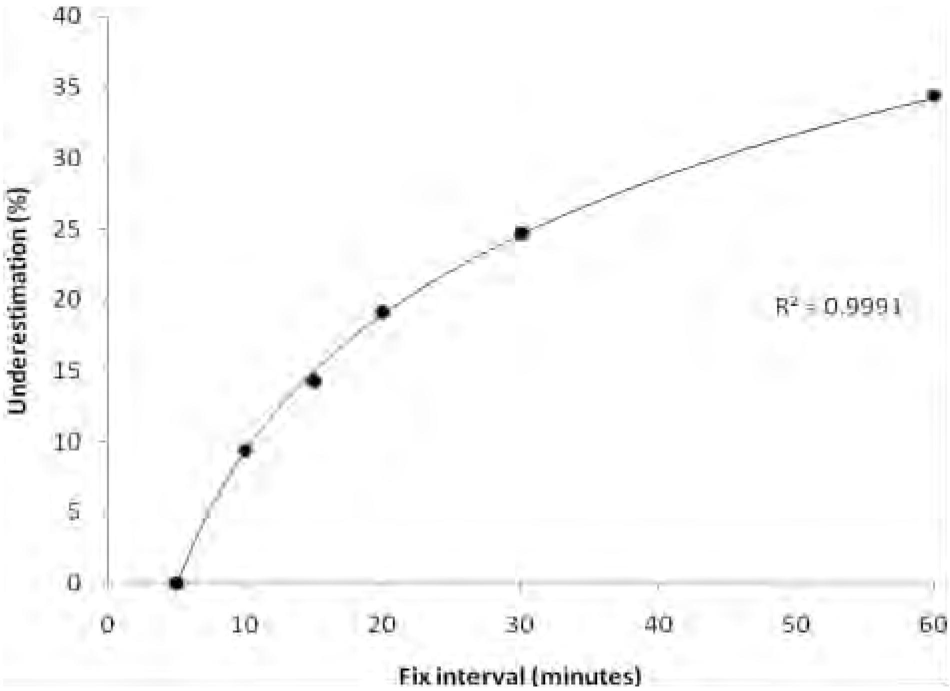


Figure 2.5: The extent to which GPS fixes at different sampling intervals underestimate crude path lengths travelled by habituated Southern Ground-Hornbills sampled every 5 minutes at the Mabula Private Game Reserve (from Dickens, 2010).

Travel distances were estimated for four seasons: Early Wet (October-December), Late Wet (January-March), Early Dry (April-June) and Late Dry (July-September). Breeding takes place during the wet season (austral summer). If a location was not obtained, the displacement estimates from fixes >1 hour apart were omitted from analyses of hourly movement. Daily movement was estimated by summing hourly displacement estimates (corrected by 38%), but estimates were discarded if there were two or more missing fixes per day. Daily travel distances were close to normally distributed and so a General Linear Model

(GLM) was run in R (R Core Team, 2014) to assess the role of season, group and breeding status on daily travel distance. A fully explicit model was run, allowing interactions among all three factors.

Hourly travel distances were related to ambient temperature using weather data for the town of Hoedspruit (SAWS, www.weathersa.co.za), the closest weather station to the APNR (~20 km from the centre of the APNR). The effects of time of day, season, group and temperature on hourly travel distance was assessed with a Generalised Additive Model (GAM) in R package 1.8-0 (Wood, 2011). Hourly distance estimates were log transformed because the data were left constrained (≥ 0) and right-skewed. Hour and Temperature were run as smoothed terms (so that they could have non-linear relationships) with Hour having an interaction term with Season, recognising the fact that the birds roost at different times of days linked to seasonal changes in day length. Season and Group were categorical terms but with an interaction term (so that Season effects need not be the same for each group).

Each group's home range and patterns of habitat use were determined using Minimum Convex Polygons (MCP) and Kernel Density Estimates (KDE; Rodgers *et al*., 2007). Daily MCPs were generated to determine patterns of habitat use. Thirty randomly selected daily MCPs were plotted to depict patterns of habitat use, while the monthly mean sequential overlap of daily MCPs was assessed to determine how patterns of habitat use change seasonally. The KDEs used a raster grid cell size of 50 m with the smoothing parameter (h_{ref}) selected using the default settings in HRT for ArcGIS® 9.3.

KDEs of the Senelala group were generated in six two-hour bins from 06:00 - 18:00 for each of the four seasons. The Senelala group was selected because their chick did not survive, meaning that the group was less restricted to habitats around the nest than other groups. The KDEs were then overlaid onto the geo-referenced vegetation map to determine whether patterns of habitat use were influenced by the midday demand for shade. Three two-hour bins from 10:00-16:00, spanning the hottest part of the day, were used to determine whether particular vegetation types were favoured over others, based on their potential to provide shade. Based on estimates of canopy occlusion, acacia woodlands (23%) and riparian habitats (13%) provide the most shade of major habitats within the APNR; other vegetation types provide less shade (8–10%) canopy occlusion). The total proportion of GPS fixes within acacia and riparian vegetation types were therefore compared throughout the day in each season.

Results

A total of 23 304 hourly GPS locations were obtained for the four groups, with 6 971 hourly fixes not recorded (23%). Daily travel distances were obtained for 1 231 group-days, with missing data for 229 group-days (16%), of which 61 days (4% overall) was a result of the Rhino Road group losing their tag in February-March 2011.

Daily travel distances

Extrapolated daily travel distances averaged 7.4 ± 2.2 km (monthly averages ranging from 4–11 km per day, Table 2.1). Season had the greatest impact on daily travel distance, but group and breeding status and the interactions among all terms also improved the model, which explained 49% of the total deviance (Table 2.2). Daily movements were greatest in the Early Wet season (October–December), with mean daily travel distances for the four groups ranging from 8.4–10.6 km (Figure 2.6). Travel distances decreased progressively throughout the Late Wet season (January–March, Table 2.1), with mean daily travel distances of 5.8–7.6 km (excluding the Rhino Road group, which lacked data for February and March). Mean daily travel distances were lowest in the Early Dry season (April-June, 5.7–6.4 km), increasing slightly in the Late Dry season (July-September, 6.3–7.9 km, Figure 2.6). Controlling for the effects of season, birds travelled slightly further when breeding than not breeding in three of the four groups, but this effect was small relative to other factors (Table 2.2). The Senelala group showed a decrease in daily travel distance earlier than the other three groups, consistent with its early breeding failure (Table 2.1, Figure 2.6).

Table 2.1: Estimated mean ± SD daily travel distances (km) of four Southern Ground-Hornbill groups throughout the year in the APNR, northeast South Africa, based on hourly GPS displacements x 1.38 (see methods for details).

		Southern Ground-Hornbill groups				All groups
Season	Month	Kharan Khaya	Keer Keer	Rhino Road	Senelala	
Early Wet	Oct	9.5 ± 1.3	8.5 ± 1.0	11.2 ± 1.4	8.2 ± 1.0	9.4 ± 1.7
	Nov	9.3 ± 1.3	9.2 ± 1.3	10.9 ± 1.4	9.8 ± 1.3	9.8 ± 1.5
	Dec	10.4 ± 1.1	8.8 ± 1.8	9.7 ± 1.4	7.3 ± 1.4	9.0 ± 1.8
Late Wet	Jan	8.6 ± 1.4	10.5 ± 1.6	10.4 ± 1.3	7.1 ± 1.2	9.1 ± 2.0
	Feb	8.4 ± 1.2	8.1 ± 1.8	No data	5.8 ± 1.2	7.4 ± 1.9
	Mar	5.7 ± 1.3	3.9 ± 0.9	No data	4.6 ± 1.2	4.7 ± 1.3
Early Dry	Apr	6.4 ± 1.0	5.9 ± 1.2	5.7 ± 1.3	5.8 ± 1.1	5.9 ± 1.2
	May	5.6 ± 1.1	6.2 ± 1.7	6.9 ± 1.0	6.4 ± 1.2	6.3 ± 1.3
	Jun	5.1 ± 0.9	6.6 ± 0.9	6.6 ± 1.3	5.5 ± 1.1	5.9 ± 1.2
Late Dry	Jul	6.2 ± 1.3	6.9 ± 1.0	8.7 ± 1.4	6.0 ± 1.4	6.9 ± 1.6
	Aug	6.0 ± 1.4	6.7 ± 1.4	7.0 ± 1.4	6.6 ± 1.9	6.6 ± 1.5
	Sep	7.0 ± 1.2	6.2 ± 1.1	8.2 ± 1.1	6.5 ± 1.4	7.0 ± 1.4
All year		7.4 ± 2.1	7.3 ± 2.2	8.5 ± 2.3	6.6 ± 1.8	7.4 ± 2.2

Table 2.2: The effects of season, group and breeding status on daily movement distances of four Southern Ground-Hornbill groups in the APNR, northeast South Africa, estimated with a GLM.

Factor	df	Deviance explained	Residual df	Residual deviance	F	P
Null model			1230	5896		
Group	3	516	1227	5380	69.0	< 0.001
Season	3	1990	1224	3391	266.0	< 0.001
Breeding status	1	69	1223	3322	27.7	< 0.001
Group * season	9	250	1214	3072	11.1	< 0.001
Group * breeding status	3	55	1211	3018	7.3	< 0.001

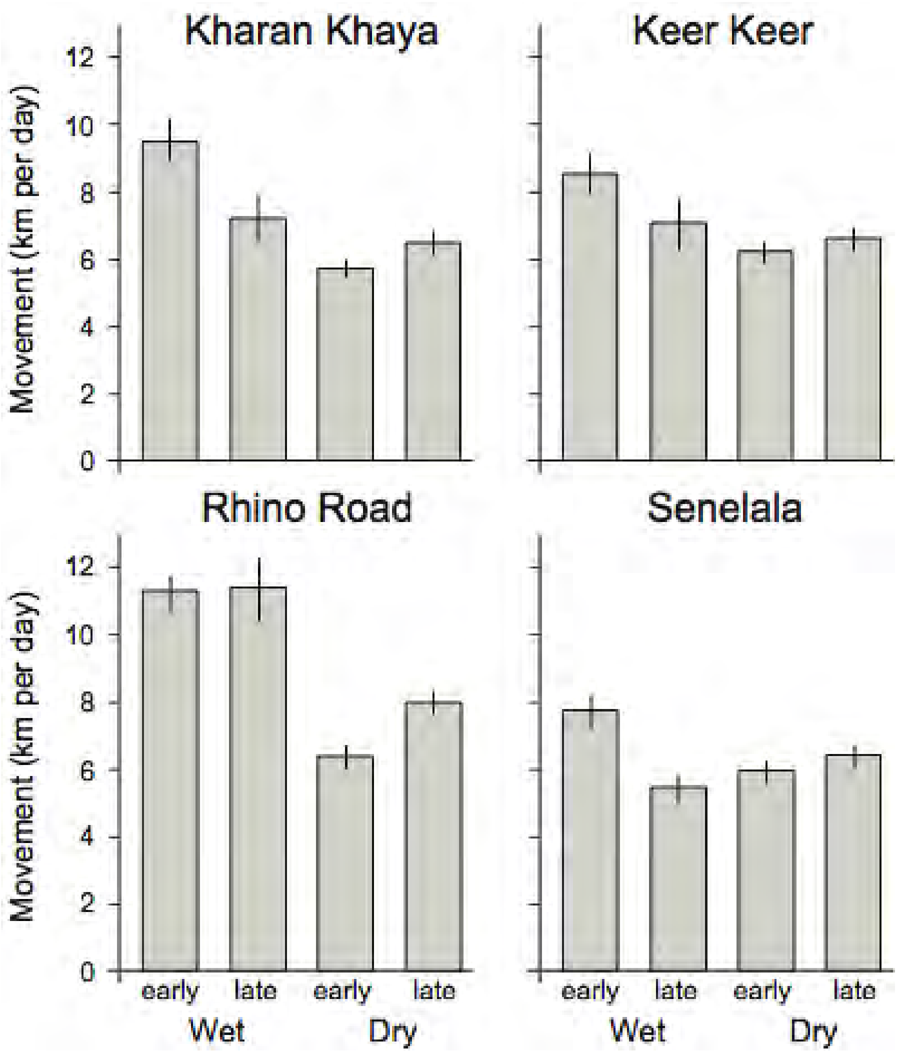


Figure 2.6: Seasonal changes in mean daily movement estimates for four Southern Ground-Hornbill groups in northeast South Africa. Error bars show 95% confidence intervals; note that the late wet season data for the Rhino Road group are only from January.

Diurnal movement patterns

Time of day, season, group, temperature and the interaction between season and group all significantly affected hourly travel distances by Southern Ground-Hornbill groups (all factors $P < 0.001$, except group $P = 0.006$). In all seasons, foraging peaked at temperatures of 10-15˚C, decreasing slightly below 10˚C and more markedly at temperatures above 20˚C. As a result, birds travelled farthest per hour in the morning, decreasing in the afternoon in winter (Figure 2.7). However, in summer hourly travel distances were bimodally distributed, with a minimum during the middle of the day when ambient temperatures exceed 25˚C (Figure 2.7, Table 2.3).

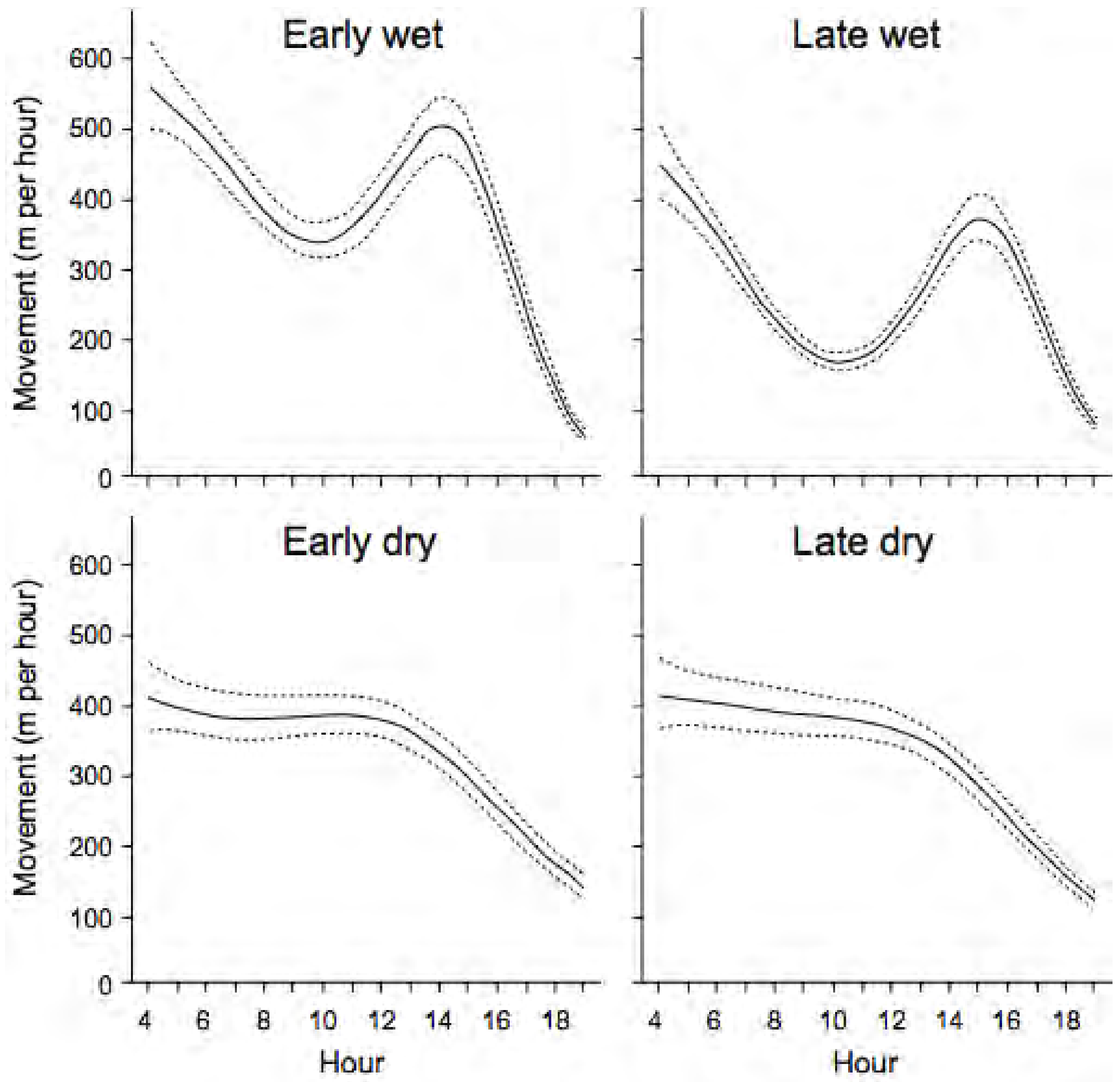


Figure 2.7: GAM plots showing seasonal differences in estimated hourly travel distances of four Southern Ground-Hornbill groups in northeast South Africa. Dashed lines show 95% confidence intervals.

Spatial foraging patterns

The three groups that bred successfully (Kharan Khaya, Keer Keer and Rhino Road) concentrated their daily foraging activity around their nests in the Early Wet and Late Wet seasons, switching to dispersed foraging in the Early Dry and Late Dry seasons (Appendices 2.4–2.7). The Senelala group, whose breeding attempt failed, did not display the same pattern, with dispersed and random foraging across all four seasons. The Senelala group utilised acacia and riparian habitat types disproportionately more during the heat of the day (10:00–16:00) than all other habitat types combined in the Early Wet and Late Wet seasons (Figures 2.8 and 2.9).

Table 2.3: Seasonal changes in mean ± SD hourly travel distances (m) by Southern Ground-Hornbills in relation to mean ambient temperatures in the APNR, northeast South Africa.

Time of day	Early Wet		Late Wet		Early Dry		Late Dry	
	m	˚C	m	˚C	m	˚C	m	˚C
04:00-05:00	837 ± 67	19.1	658 ± 73	20.0	438 ± 92	12.9	336 ± 65	11.7
05:00-06:00	847 ± 144	19.0	766 ± 163	19.8	543 ± 77	12.7	436 ± 105	11.4
06:00-07:00	801 ± 132	19.5	690 ± 170	19.8	572 ± 37	12.4	605 ± 137	11.2
07:00-08:00	714 ± 169	21.2	664 ± 236	21.0	610 ± 89	12.8	681 ± 50	12.0
08:00-09:00	621 ± 114	22.8	496 ± 140	22.9	569 ± 85	16.1	604 ± 50	15.3
09:00-10:00	591 ± 45	24.2	402 ± 91	24.4	516 ± 38	18.8	538 ± 71	18.7
10:00-11:00	543 ± 75	27.3	377 ± 81	26.1	492 ± 43	20.9	528 ± 81	20.8
11:00-12:00	495 ± 68	29.7	351 ± 24	28.5	482 ± 64	22.2	546 ± 107	21.2
12:00-13:00	478 ± 68	31.2	400 ± 75	29.5	446 ± 93	23.3	484 ± 95	22.4
13:00-14:00	478 ± 68	31.3	412 ± 89	31.3	451 ± 63	24.6	484 ± 105	23.1
14:00-15:00	535 ± 46	30.8	450 ± 86	31.5	466 ± 43	24.3	584 ± 94	23.0
15:00-16:00	668 ± 70	30.6	610 ± 86	31.0	562 ± 60	23.4	603 ± 94	22.7
16:00-17:00	635 ± 106	30.0	678 ± 126	29.6	417 ± 26	23.2	563 ± 71	22.1
17:00-18:00	663 ± 100	28.4	625 ± 178	28.7	401 ± 55	21.1	510 ± 103	21.2
18:00-19:00	600 ± 78	26.4	615 ± 139	26.6	348 ± 49	18.7	402 ± 110	19.7
19:00-20:00	572 ± 160	24.3	544 ± 90	24.0	317 ± 40	17.1	283 ± 11	17.7

The three groups that bred successfully in 2010/11 showed a high degree of foraging area overlap on successive days during the breeding season (Early Wet and Late Wet seasons), with an average of 64–67% overlap in MCPs during the Early Wet and 62–64% during the Late Wet season (Figure 2.10). By comparison, the Senelala group, which failed to raise a chick, had only 42% mean sequential overlaps in MCPs in the Early Wet season and 17% overlap in the Late Wet season. Overlap in daily foraging areas for all groups was low in the Early Dry (15-20%) and Late Dry (9-18%) seasons.

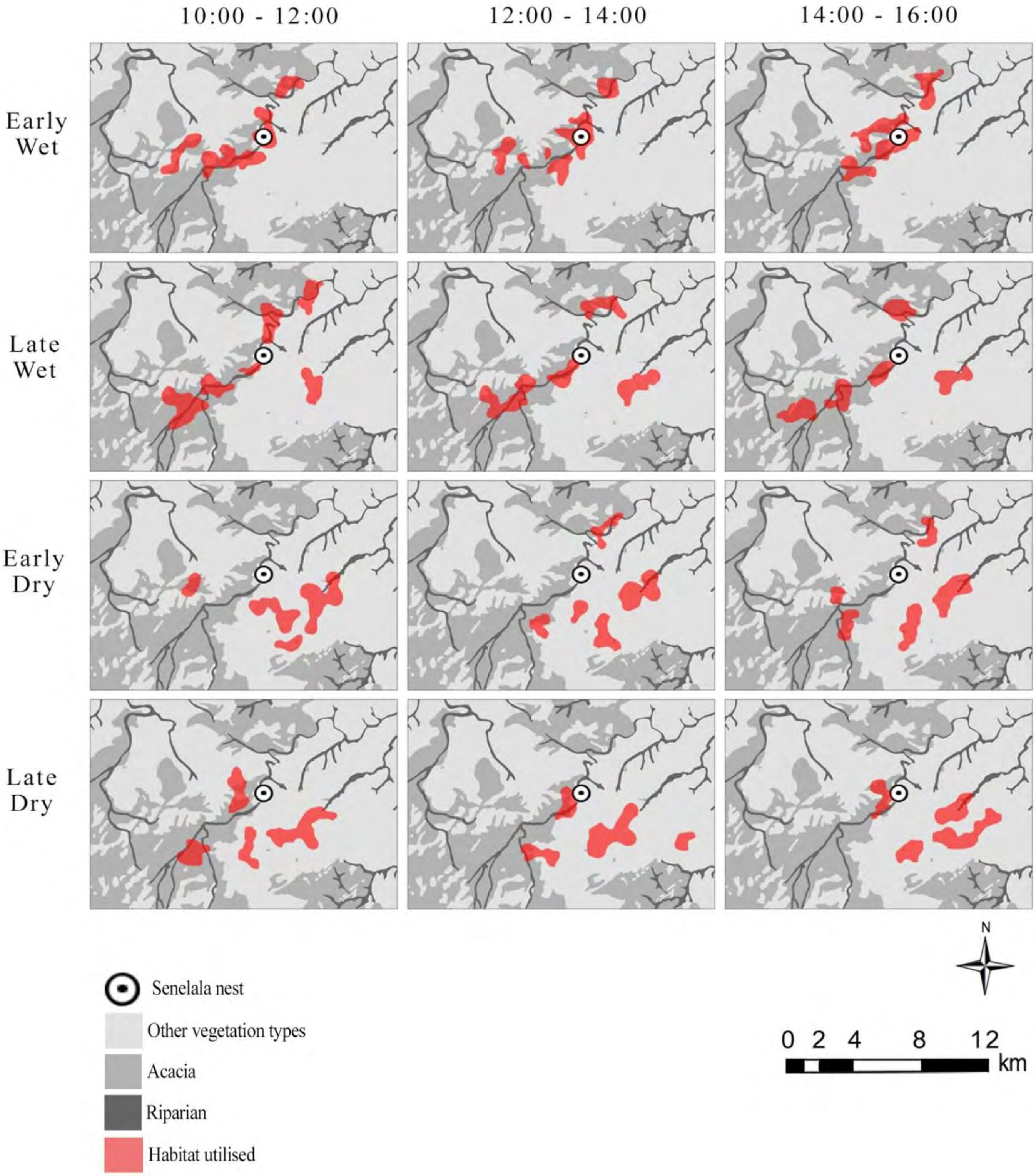


Figure 2.8: Spatio-temporal patterns of habitat use during the heat of the day per season by the Senelala Southern Ground-Hornbill group which failed to breed successfully during the study period.

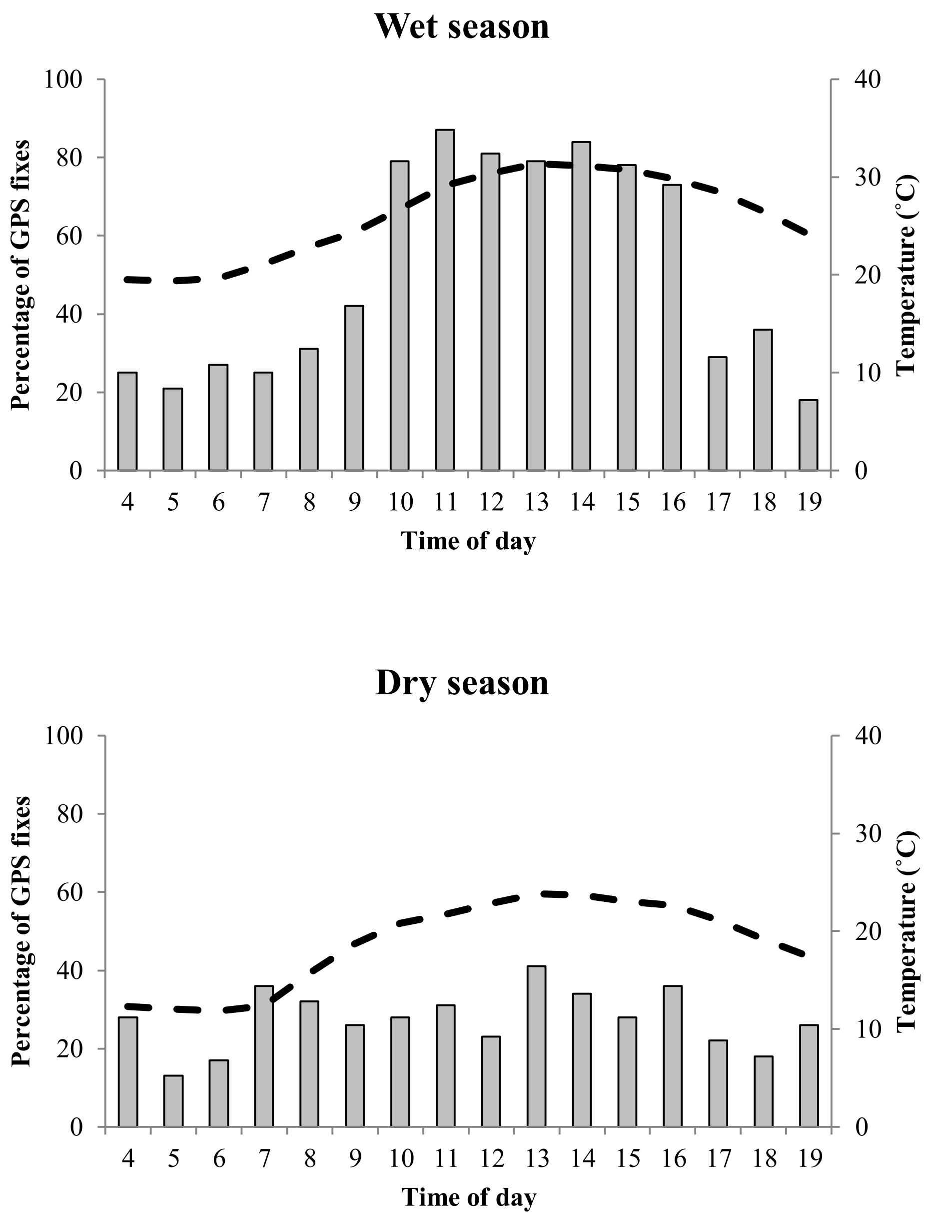


Figure 2.9: Seasonal differences in the daily patterns of use of shaded habitats (acacia and riparian woodland) by the Senelala Southern Ground-Hornbill group. Histogram = time spent in shaded habitats; dashed line = average ambient temperature.

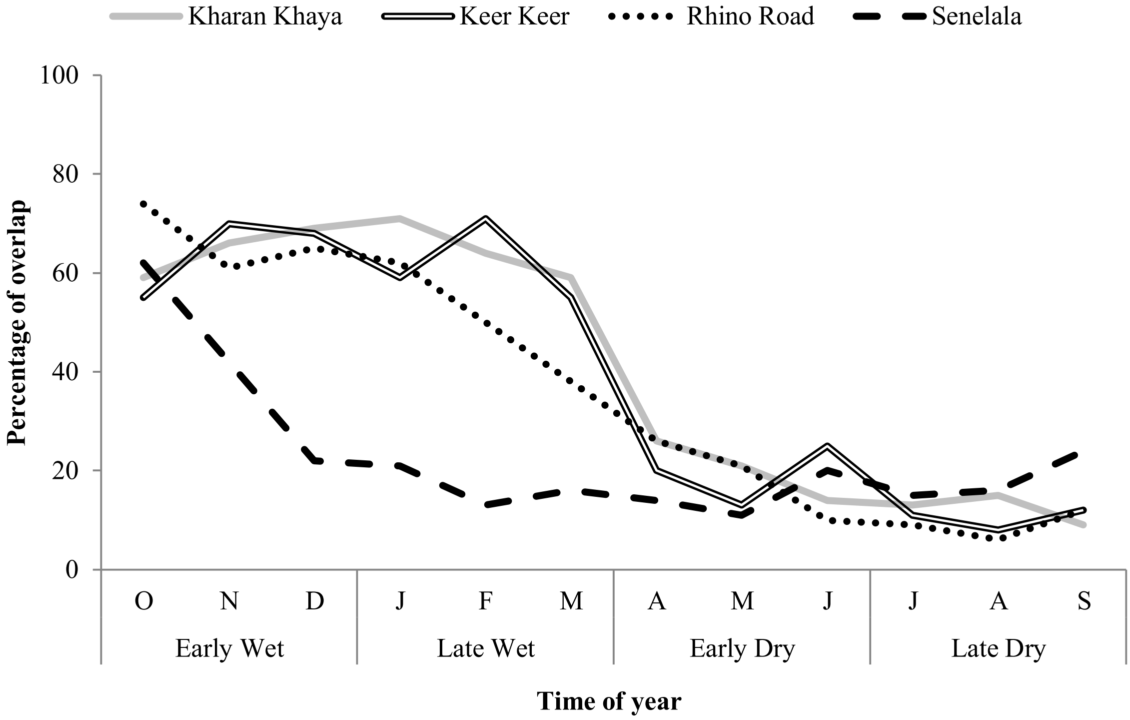


Figure 2.10: Monthly mean sequential overlap of daily Minimum Convex Polygons of the foraging patterns of four Southern Ground-Hornbill groups throughout the year in the APNR, northeast South Africa.

Discussion

Ground-hornbill prey are likely to be more abundant in the wet, warm summer months, so we might expect ground-hornbills to travel further to find food in the dry season when food is less abundant and more patchily distributed (Pyke, 1984; Rautenbach *et al*., 1988; Linzey & Kesner, 1997). However, ground-hornbill groups travelled further each day during summer. This might reflect in part the greater day length in summer. However, summer also is the period of peak breeding activity, when the group has to make numerous trips to and from the nest to provision the incubating alpha female and the growing chick (Kemp, 1995). The Senelala group had their lowest mean daily travel distances in the Late Wet season, after their breeding attempt had failed, suggesting that resources are indeed more abundant in summer.

The three groups that raised a chick in 2010/11 all exhibited their lowest mean daily travel distances in the Early Dry season. This period coincides with when the chicks fledge, and have to travel with the group for the first time. The lower mean daily travel distances may result from the group moving more slowly due to the presence of the newly fledged chick, which might take some time to acquire fitness and endurance, and also when group members are recovering from the breeding effort (cf. Weimerskirch *et al*., 2006). Chicks are largely dependent on group members for food for the first six months to a year after fledging (Kemp & Kemp, 1991; Kemp, 1995).

Temperature played a key role in movement distances, especially in the hot, wet summer months (wet season). Groups travelled farthest when ambient temperatures were cool (10-15˚C), and distances covered decreased markedly at temperatures above 25˚C. The first signs of heat-dissipation behaviour by Southern Ground-Hornbills (including reducing activity or stopping to rest in areas of shade) occur at temperatures >25˚C (Kemp & Kemp, 1980). Heat stress is a function of temperature and insolation (Kemp & Kemp, 1980; Walsberg *et al*., 1997). Insolation peaks at midday (Kemp & Kemp, 1980; Walsberg *et al*., 1997), which may explain why travel distances increase slightly after midday despite temperatures remaining > 25˚C (Table 2.3). The type of habitat used also is affected by temperature. Most foraging takes place in open habitats, but when temperatures exceeded 25˚C (mainly in summer), ground-hornbills spent much more time in dense acacia and riparian woodland where they can reduce exposure to sunlight. Riparian habitats might also offer some moderating effect on temperature due to the presence of water. The sensitivity of ground-hornbills to high temperatures is typical of large birds (McKechnie & Wolf, 2009), but is worrying in the face of climatic warming, especially given the relatively modest temperature at which the birds appear heat-stressed.

Home range was influenced by breeding activity, with breeding groups foraging in a zone around the nest site, whereas nonbreeding groups disperse over a much greater area. Foraging groups have to 'decide' whether to travel further in search of more rewarding habitats, based on gross foraging returns, or to remain nearby in potentially less rewarding habitats, based on the travel costs involved (Bino *et al*., 2010). Central place foraging constrains this tradeoff in breeding groups, which have to compromise between gross foraging returns and the travel costs involved in having to constantly travel to and from the nest carrying food (Rautenbach *et al*., 1988; Linzey & Kesner, 1997).

The results confirm that ground-hornbills require a large home range, but within this range, the location of the nest site is crucial as foraging is constrained to the vicinity of the nest during the breeding season. It is thus essential that the area around the nest offers both open areas for foraging as well shaded areas to avoid overheating. This insight is important when assessing habitat management options for the species and particularly for the placement of artificial nests.

Appendices

Appendix 2.1: Vegetation types of the APNR, northeast South Africa after Van Rooyen *et al.* (2005).

1. *Ficus abutilifolia - Ochna inermis* rocky outcrops and ridges, and dolerite dykes
2. *Combretum apiculatum - Sclerocarya birrea* open woodland
3. *Terminalia sericea - Combretum zeyheri* woodland
4. *Terminalia sericea - Combretum zeyheri - Pterocarpus rotundifolius* - open woodland
5. *Combretum apiculatum - Sclerocarya birrea - Strychnos madagascariensis* open woodland
6. *Combretum apiculatum - Xerophyta retinervis* low thicket
7. *Combretum apiculatum - Grewia bicolor* low thicket
8. *Combretum apiculatum - Terminalia prunioides* rugged veld
9. *Acacia nigrescens - Combretum apiculatum* mixed woodland
10. *Acacia nigrescens - Terminalia prunioides* woodland
11. *Colophospermum mopane - Combretum apiculatum* woodland
12. *Colophospermum mopane* dense woodland and shrubveld (thicket)
13. *Spirostachys africana - Euclea undulata* mixed alluvial savanna
14. *Acacia tortilis* lowland woodland
15. *Euclea divinorum - Sporobolus ioclados* short woodland on saline lowlands and floodplains
16. *Acacia luederitzii - Euclea divinorum* lowland woodland
17. *Albizia harveyi - Combretum hereroense - Acacia gerrardii - Euclea divinorum* lowland woodland
18. *Acacia nigrescens - Combretum hereroense* open woodland
19. *Acacia gerrardii - Euclea divinorum - Sporobolus nitens* lowland savanna
20. *Acacia gerrardii - Combretum hereroense* lowland savanna
21. *Schotia brachypetala - Philenoptera violacea* riparian woodland
22. *Phragmites australis* reedbeds

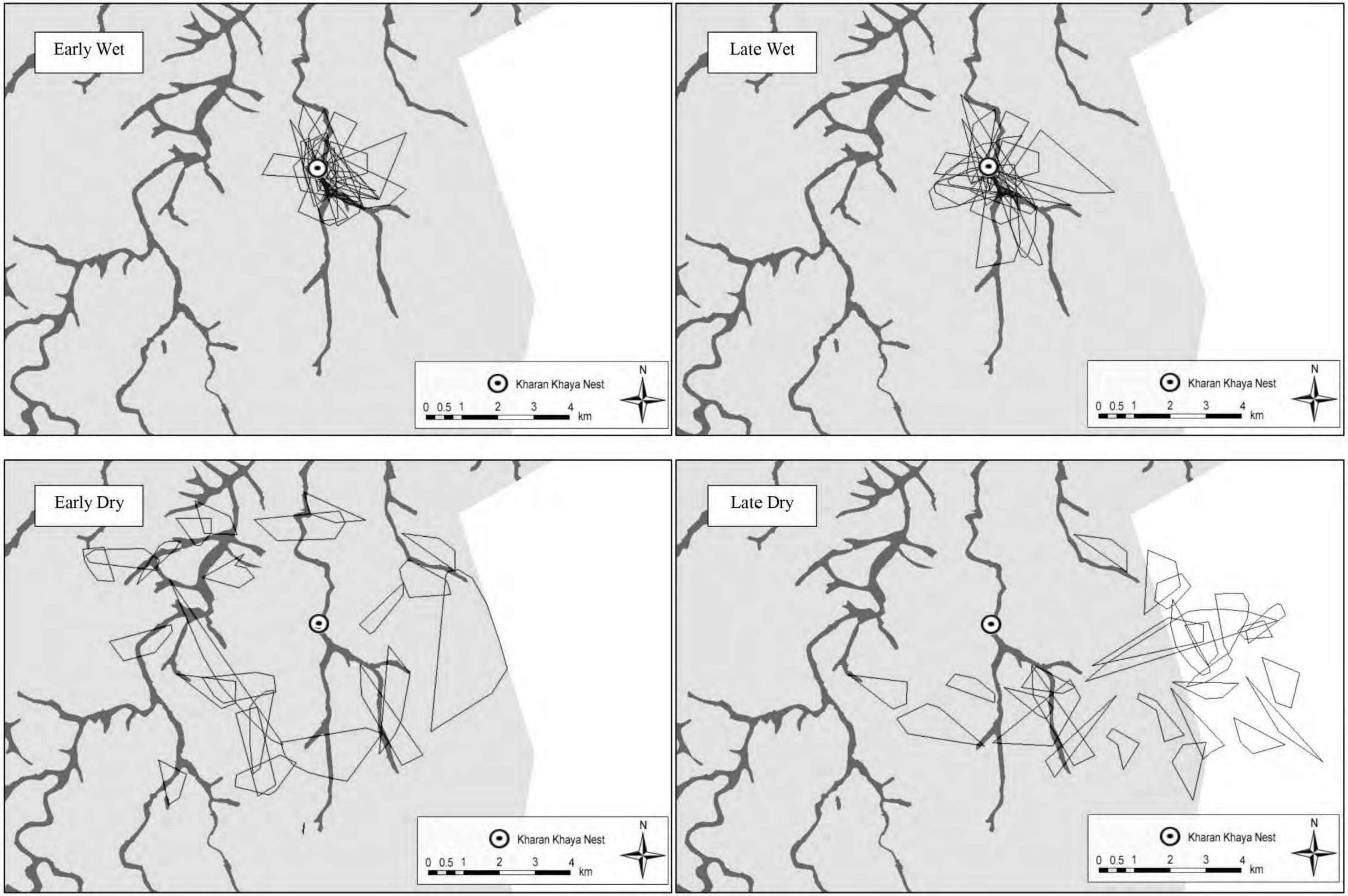
Appendix 2.2: Observed and corrected mean daily travel distances (km) of four Southern Ground-Hornbill groups throughout the year in the APNR, northeast South Africa.

Season	Month	Kharan Khaya		Keer Keer		Rhino Road		Senelala		Groups combined	
		Observed	Corrected	Observed	Corrected	Observed	Corrected	Observed	Corrected	Observed	Corrected
Early Wet	October	6.7	9.3	6.3	8.7	8.1	11.2	5.9	8.1	6.8	9.3
	November	6.8	9.4	6.5	9.0	7.9	11.0	7.1	9.7	7.1	9.8
	December	7.4	10.3	6.4	8.8	7.2	9.9	5.6	6.5	6.7	8.9
Late Wet	January	6.0	8.4	8.0	11.1	7.7	10.6	5.1	6.3	6.7	9.1
	February	6.2	8.6	5.6	7.7	No data	No data	4.1	5.6	5.3	7.3
	March	3.9	5.5	2.9	3.9	No data	No data	3.2	4.4	3.3	4.6
Early Dry	April	4.6	6.4	4.4	6.1	4.0	5.5	4.2	5.9	4.3	5.9
	May	4.2	5.8	4.4	6.1	4.9	6.7	4.6	6.4	4.5	6.3
	June	3.6	5.0	4.6	6.4	4.8	6.7	3.9	5.4	4.2	5.9
Late Dry	July	4.6	6.3	5.0	6.9	6.1	8.4	4.3	6.0	5.0	6.9
	August	4.3	5.9	4.7	6.4	5.0	6.9	4.7	6.5	4.7	6.4
	September	5.0	7.0	3.9	6.2	5.9	8.1	4.7	6.4	4.9	6.9
	Yearly mean	5.3	7.3	5.2	7.3	6.2	8.5	4.8	6.4	5.3	7.3

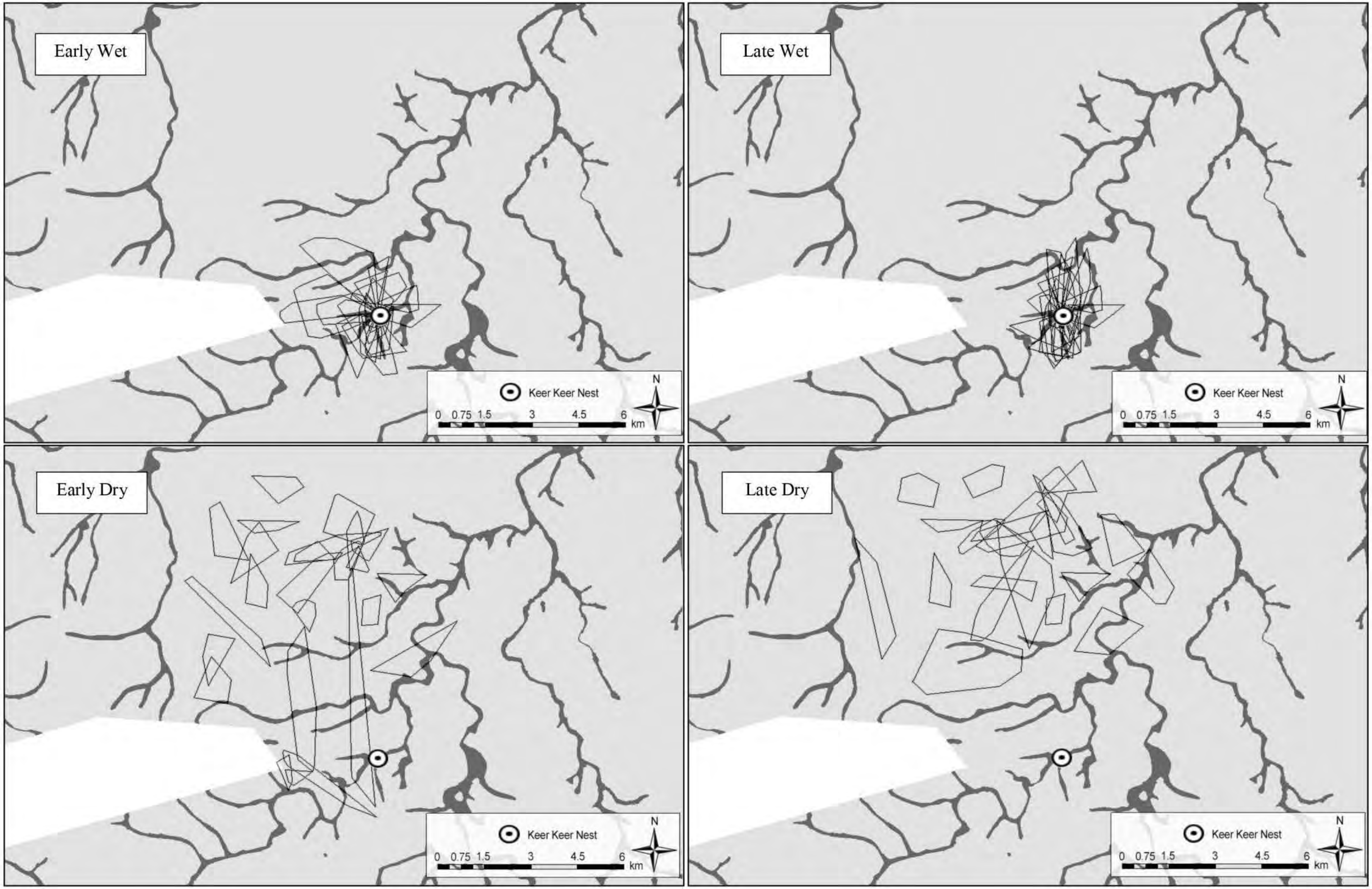
Appendix 2.3: Mean hourly travel distance (Travel = m) of four Southern Ground-Hornbill groups and mean hourly temperature (Temp = ˚C) throughout the year in the APNR, northeast South Africa.

	Season							
	Early Wet		Late Wet		Early Dry		Late Dry	
Time of day	Travel	Temp	Travel	Temp	Travel	Temp	Travel	Temp
04:00	837 ± 67	19.1 ± 0.93	658 ± 73	20.0 ± 0.60	438 ± 92	12.9 ± 4.25	336 ± 65	11.7 ± 2.82
05:00	847 ±144	19.0 ± 0.87	766 ± 163	19.8 ± 0.61	543 ± 77	12.7 ± 4.25	436 ± 105	11.4 ± 2.97
06:00	801 ± 132	19.5 ± 1.21	690 ± 170	19.8 ± 0.75	572 ± 37	12.4 ± 4.41	605 ± 137	11.2 ± 3.17
07:00	714 ± 169	21.2 ± 1.17	664 ± 236	21.0 ± 0.60	610 ± 89	12.8 ± 4.65	681 ± 50	12.0 ± 3.76
08:00	621 ± 114	22.8 ± 1.10	496 ± 140	22.9 ± 0.66	569 ± 85	16.1 ± 3.56	604 ± 50	15.3 ± 4.09
09:00	591 ± 45	24.2 ± 1.05	402 ± 91	24.4 ± 0.87	516 ± 38	18.8 ± 1.95	538 ± 71	18.7 ± 3.23
10:00	543 ± 75	27.3 ± 0.75	377 ± 81	26.1 ± 1.07	492 ± 43	20.9 ± 1.32	528 ± 81	20.8 ± 3.16
11:00	495 ± 68	29.7 ± 0.68	351 ± 24	28.5 ± 1.14	482 ± 64	22.2 ± 1.31	546 ± 107	21.2 ± 3.39
12:00	478 ± 68	31.2 ± 0.26	400 ± 75	29.5 ± 1.37	446 ± 93	23.3 ± 1.34	484 ± 95	22.4 ± 3.52
13:00	478 ± 68	31.3 ± 0.40	412 ± 89	31.3 ± 1.54	451 ± 63	24.6 ± 1.31	484 ± 105	23.1 ± 3.61
14:00	535 ± 46	30.8 ± 0.45	450 ± 86	31.5 ± 1.61	466 ± 43	24.3 ±1.17	584 ± 94	23.0 ± 3.73
15:00	668 ± 70	30.6 ± 0.57	610 ± 86	31.0 ± 1.47	562 ± 60	23.4 ± 0.96	603 ± 94	22.7 ± 3.62
16:00	635 ± 106	30.0 ± 0.52	678 ± 126	29.6 ± 1.59	417 ± 26	23.2 ± 1.02	563 ± 71	22.1 ± 3.66
17:00	663 ± 100	28.4 ± 0.30	625 ± 178	28.7 ± 1.22	401 ± 55	21.1 ± 1.64	510 ± 103	21.2 ± 3.90
18:00	600 ± 78	26.4 ± 0.35	615 ± 139	26.6 ± 0.60	348 ± 49	18.7 ± 2.75	402 ± 110	19.7 ± 4.05
19:00	572 ± 160	24.3 ± 0.15	544 ± 90	24.0 ± 0.47	317 ± 40	17.1 ± 3.10	283 ± 11	17.7 ± 3.36

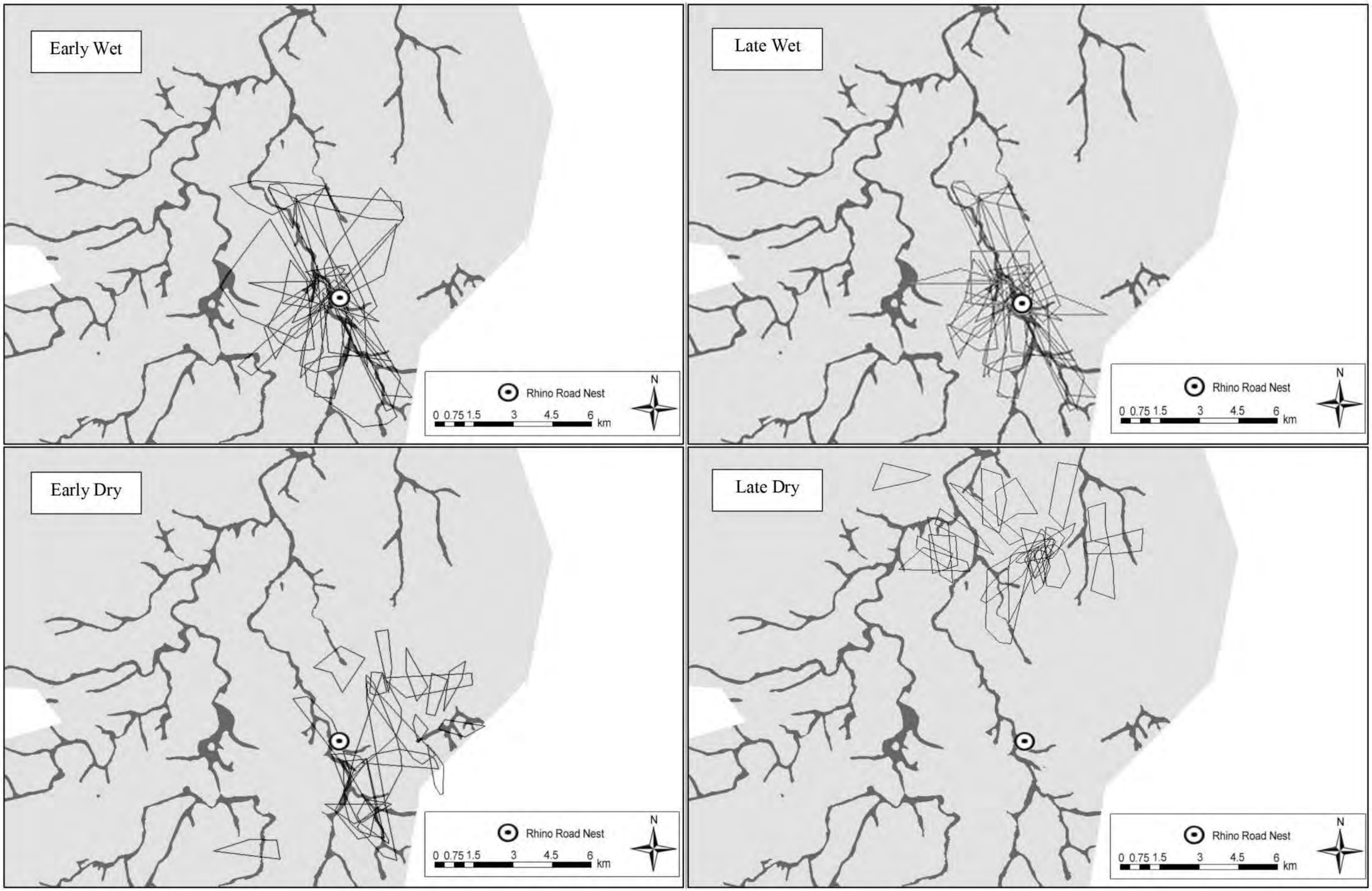
Appendix 2.4: Thirty randomly selected Minimum Convex Polygons for the seasonal daily foraging patterns of the Kharan Khaya Southern Ground-Hornbill group in the APNR, northeast South Africa. Dark grey shading represents riparian habitat and light grey shading represents all other habitat types combined.



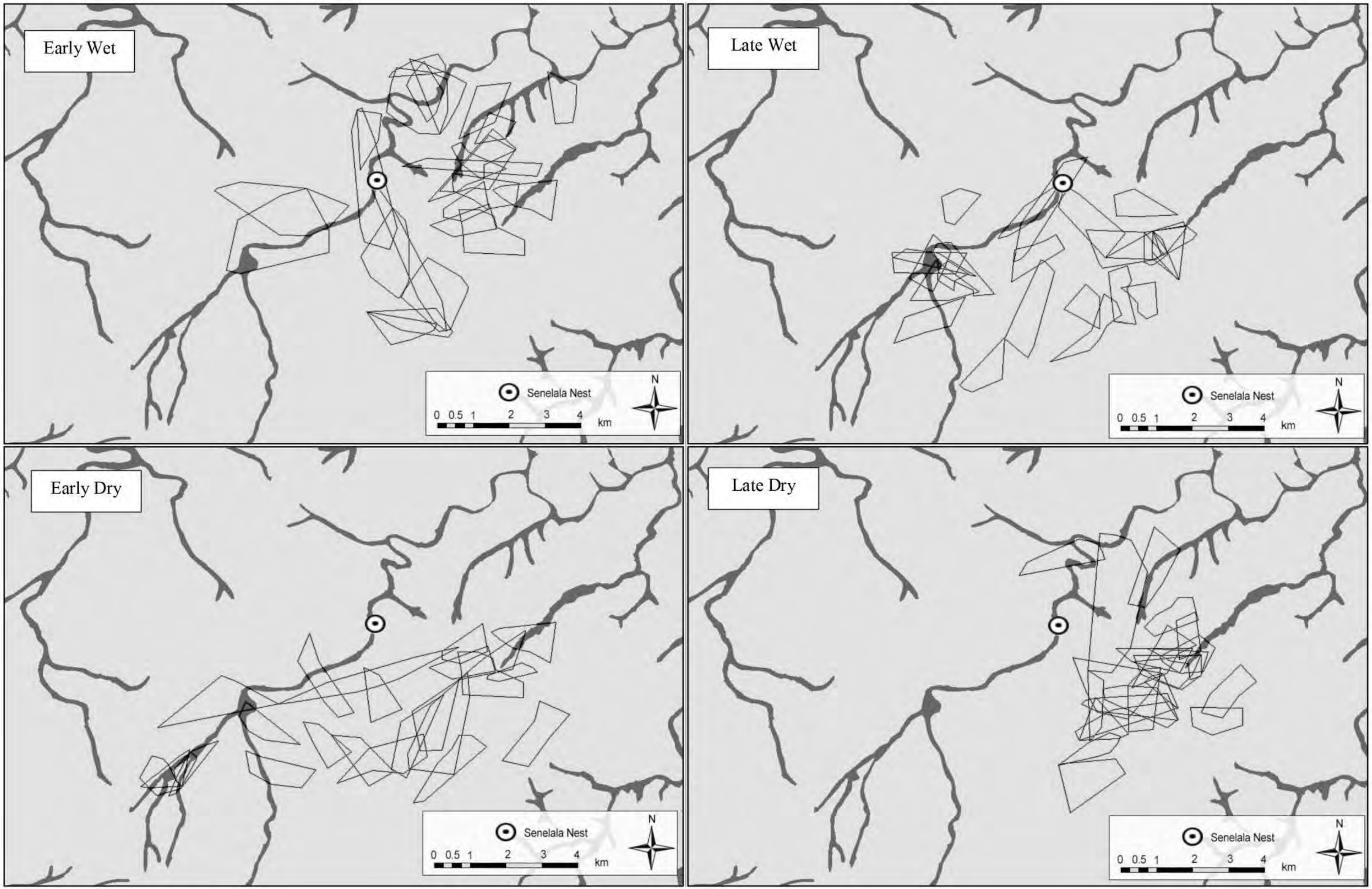
Appendix 2.5: Thirty randomly selected Minimum Convex Polygons for the seasonal daily foraging patterns of the Keer Keer Southern Ground-Hornbill group in the APNR, northeast South Africa. Dark grey shading represents riparian habitat and light grey shading represents all other habitat types combined.



Appendix 2.6: Thirty randomly selected Minimum Convex Polygons for the seasonal daily foraging patterns of the Rhino Road Southern Ground-Hornbill group in the APNR, northeast South Africa. Dark grey shading represents riparian habitat and light grey shading represents all other habitat types combined.



Appendix 2.7: Thirty randomly selected Minimum Convex Polygons for the seasonal daily foraging patterns of the Senelala Southern Ground-Hornbill group in the APNR, northeast South Africa. Dark grey shading represents riparian habitat and light grey shading represents all other habitat types combined.



CHAPTER 3

PATTERNS OF ROOST SITE SELECTION AND USE BY SOUTHERN GROUND-HORNBILLS IN THE SOUTH AFRICAN LOWVELD

Abstract

Different habitats may be used for various aspects of an animal's life. Southern Ground-Hornbill *Bucorvus leadbeateri* breeding groups defend year-round territories by pre-dawn vocalisations from their over-night roost sites. Knowledge on ground-hornbill roosting habits is limited; groups roost in large trees, apparently where they end up after daily foraging. In this chapter I report patterns of roost site selection and use for four ground-hornbill groups in the Associated Private Nature Reserves, northeast South Africa, based on data from GPS-satellite tags. The number of roost sites used per month averaged 15.4 ± 4.7 across all groups, indicating little evidence of strong preferences for specific sites. This number was least when breeding, decreasing throughout the Early Wet season (October-December) and lowest during the Late Wet season (January–March) when all groups frequently roosted close to the nest site (54–83% of roosts within <1 000 m of the nest). As might be expected therefore, the mean monthly number of nights per roost peaked in December and January. During the breeding season, riparian habitats were favoured for roosting, whereas disturbed areas, combretum-dominated habitats and mopane-dominated habitats were used during the dry season. Adequate large trees for nesting and roosting, particularly in riparian habitats, may therefore be an important and potentially limiting factor for the successful reproduction of Southern Ground-Hornbills.

Introduction

A roost site is a location where birds settle or congregate to rest/sleep (Beauchamp, 1999). Roosts are often specific in form and are selected for their ability to provide protection against potential predation and from the elements, as well as by how conveniently placed they are to nearby foraging areas or the nest (Kemp, 1995). Birds roost singly or communally, with communal roosts providing added benefits, including a reduction in thermoregulatory demands, a decrease in individual predation risk and increased foraging efficiency, since unsuccessful foragers can follow more successful companions to optimal foraging areas (Beauchamp, 1999). Many territorial bird species have favoured roost sites within their home-range which are used frequently, returning over long distances at the end of each day, while others change roost sites on a daily basis (Kemp, 1995; Khan & Zanneer, 2010).

Roosting habits and patterns of roost site use of the Southern Ground-Hornbill *Bucorvus leadbeateri* have not been described in detail (Jordan, 2011). The species is not known to make use of regular roosts, with groups simply said to roost in large trees where they end up after the days foraging, possibly because the energetic cost of returning each night to the same roost site is prohibitive (Kemp & Kemp, 1980; Kemp, 1995). The time at which the species goes to roost varies throughout the year in relation to the time of sunset, with Southern Ground-Hornbills also suspected of mock-roosting, where birds enter an apparent roost site at dusk and squat as if to sleep, only to fly off before complete darkness to a final roost site several hundred metres away, possibly in an effort to confuse potential predators which may watch the birds settling down for the night (Kemp, 1995).

This study increases our knowledge of the roosting habits and patterns of roost site use of the Southern Ground-Hornbill by investigating (1) the number of roost sites utilised per season, (2) the frequency of use of roost sites per season, (3) the mean distance between roost sites and the nest per season, and (4) roost site location in relation to the habitat type in which they occur. I predicted that during the breeding season, when the alpha female is restricted to roosting in the nest, the alpha male and other group members will roost nearby.

Study site and Methods

The study site was the Associated Private Nature Reserves (APNR) complex of privately owned nature reserves in the Limpopo Province, South Africa (Chapter 2). The study used GPS telemetry data (fixes) for individuals from four Southern Ground-Hornbill groups followed for one year from October 2010 to September 2011. The capture method, details of tracking device and attachment, and the collection and analysis of data are described in Chapter 2. All four groups attempted to breed in the 2010/11 breeding season, but the Senelala groups' chick died during November, freeing this group to roam more widely than the other three groups that bred successfully that year (Chapter 2).

Southern Ground-Hornbills ascend to their over-night roost before dark and only descend at first light (Kemp & Kemp, 1980). Roost sites were therefore identified as GPS fixes that occurred between sunset and sunrise. Sunset and sunrise times were based on mean monthly nautical dusk and dawn times collected by the South African Weather Service (SAWS – www.weathersa.co.za) for Hoedspruit (Appendix 3.1), the closest weather station to the APNR (~20 km from the centre of the APNR). Sites more than 50 m apart were considered to be different roosts. Confirmed roost sites were then overlaid onto the geo-referenced vegetation map of the APNR and analysed using ArcGIS® 9.3.

The number of individual roost sites utilised per season and the frequency of use of roost sites were determined for each of the four seasons defined on the basis of rainfall seasonality (Chapter 2) to quantify and better understand the importance of individual roost sites for the species and to assess whether seasonal patterns of roost site use exist. Each roost site was only considered once when calculating the number of roost sites utilised per season. The mean number of nights spent at each roost site and the mean number of successive nights at each individual roost site were used to determine the frequency of use of roost sites per season. ANOVA (one-way) tests, calculated at a 5% significance level, were used to determine differences between the four groups. Roost information was not available for the Rhino Road group in February and March, because the GPS device fell off the bird and was only reattached in April. As a result, only January data were available for the Late Wet season for this group.

The mean distance between roost sites and the nest was calculated per season to determine whether seasonal patterns exist throughout the year. The distance between roost sites and the nest was recorded as one of four distance categories (0–500, 500–1 000, 1000 –2 500 and >2 500 m). Distances were analysed using ArcGIS® 9.3 and corrected according to findings by Dickens (2010; see Chapter 2). The mean distance between nightly roost sites was also calculated to determine seasonal movement patterns in relation to roost sites.

The habitat type for each roost site was identified using the geo-referenced vegetation map of the APNR in ArcGIS® 9.3 to determine whether habitat preference for roost sites exists. Two analyses were conducted: one in the breeding season (October-March), when groups were predicted to be constrained to habitats around the nest, and one for the non-breeding period (April-September), when groups were free to range throughout their territories. Selection (*Ei*) for specific habitat types was determined using a modification of Ivlev's Index (Ivlev, 1961):

$$E_i = (r_i - p_i) / (r_i + p_i)$$

where r_i = the percentage of roost sites utilised within a habitat type and p_i = the percentage of that habitat type within the group's home range. E_i values range from +1 to -1 (Ivlev, 1961), and although the index has no statistical properties, values >0.25 were considered to show preference for a habitat type and values < -0.25 were considered to show avoidance of a habitat type. E_i values between -0.25 and 0.25 were considered to show a neutral attraction for a habitat type.

Results

A total of 4 867 hourly GPS locations were obtained for the four groups between sunset and sunrise. Roosting events were obtained for 1 323 group-nights, with missing data for 137 group-nights (10%), of which 59 (4% overall) was a result of the Rhino Road group losing their tag in February-March 2011.

Number of roost sites

The number of roost sites utilised per month decreased progressively throughout the Early Wet season (October-December) for the three groups that bred successfully (Kharan Khaya, Keer Keer and Rhino Road, Figure 3.1). These groups used the lowest number of roost sites during the Late Wet season (January–March). Interestingly, the Senelala group (whose breeding attempt failed) showed an increase in the number of roost sites utilised during the Early Wet season and made use of more roost sites per month in the Late Wet season than the other three groups. The mean number of roost sites utilised throughout the dry season increased following the Late Wet season for those groups who bred successfully, while for the Senelala group, the mean number of roost sites utilised remained similar. The mean number of roost sites utilised per month across all four groups for the year was 15.4 ± 4.7.

Seasonal frequency of use of roost sites

Mean monthly nights per roost were higher for the Kharan Khaya, Keer Keer and Rhino Road group in the Early Wet and Late Wet seasons, specifically over December and January coinciding with the peak breeding period (Table 3.1). The failed Senelala group spent fewer nights per roost over the same period. Mean monthly nights per roost in the Early Dry and Late Dry seasons decreased from the Late Wet season for the three successful groups and were similarly low across all four groups. The mean monthly nights per roost of all four groups were not significantly different ($F_{3,42} = 0.96$, $p = 0.42$), with a monthly mean of 1.9 ± 0.9 nights per roost across all four groups throughout the year.

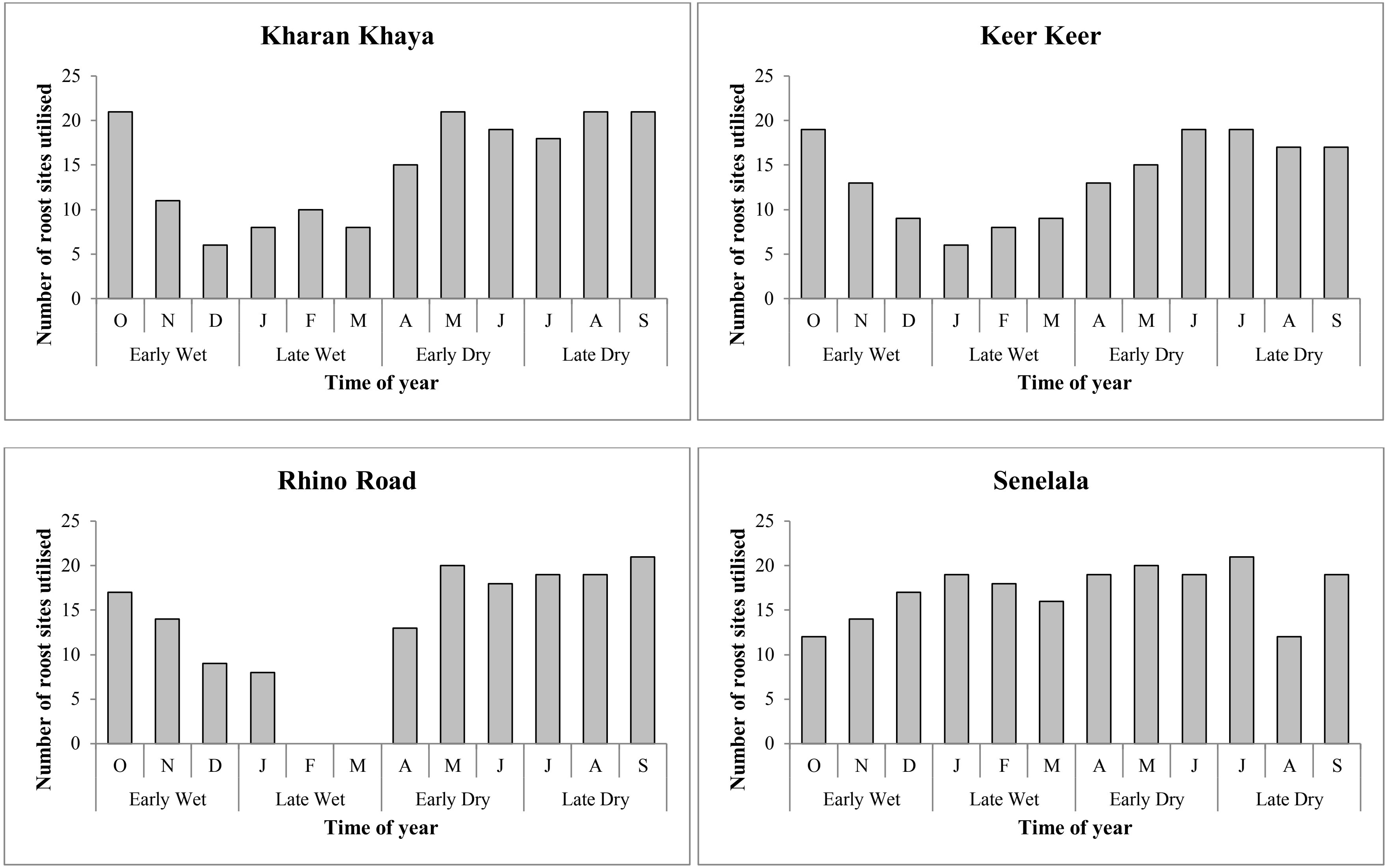


Figure 3.1: Number of roost sites utilised per month by four Southern Ground-Hornbill groups throughout the year in the APNR, northeast South Africa.

Table 3.1: Seasonal changes in mean ± SD nights per roost of four Southern Ground-Hornbill groups in the APNR, northeast South Africa.

	Southern Ground-Hornbill groups			
Season	Kharan Khaya	Keer Keer	Rhino Road	Senelala
Early Wet	2.7 ± 1.8	2.1 ± 1.0	2.1 ± 0.9	1.9 ± 0.3
Late Wet	3.3 ± 0.5	3.5 ± 1.0	4.1*	1.4 ± 0.2
Early Dry	1.5 ± 0.5	1.7 ± 0.5	1.4 ± 0.4	1.5 ± 0.4
Late Dry	1.3 ± 0.2	1.3 ± 0.2	1.3 ± 0.2	1.6 ± 0.6

*data available for month of January only.

Although no obvious seasonal variations exist, mean successive nights per roost were highest in December for the three groups that bred successfully, consistent with peak breeding. Mean successive nights per roost were not significantly different ($F_{3,42}$ = 1.94, p = 0.14) throughout the year, with a mean monthly total of 1.4 ± 0.7 nights per roost across all four groups (Table 3.2).

Table 3.2: Seasonal changes in mean ± SD number of successive nights per roost of four Southern Ground-Hornbill groups in the APNR, northeast South Africa.

	Southern Ground-Hornbill groups			
Season	Kharan Khaya	Keer Keer	Rhino Road	Senelala
Early Wet	2.5 ± 1.5	2.0 ± 1.1	1.7 ± 0.4	1.6 ± 0.4
Late Wet	2.3 ± 0.9	0.9 ± 0.3	1.7*	1.1 ± 0.1
Early Dry	1.2 ± 0.1	1.0 ± 0.2	1.3 ± 0.2	1.1 ± 0.1
Late Dry	1.2 ± 0.1	1.2 ± 0.1	1.2 ± 0.2	1.2 ± 0.2

*data available for month of January only.

Mean distance between roost sites and the nest per season

Throughout the Early Wet season, all four groups frequently roosted in close proximity to the nest, with 54–83% of roosts being within 1 000 m of the nest (Figure 3.2). In the Late Wet season, those groups who bred successfully increasingly used roosts within 1 000 m of the nest (88–100%), while the Senelala group no longer roosted near the nest, consistent with its early breeding failure, with only 12% of roosts within 1 000 m of the nest. Throughout the Early Dry and Late Dry seasons, all four groups roosted away from the nest, with 71-82% and 66-82% of roosts for the respective seasons being >2 500 m from the nest.

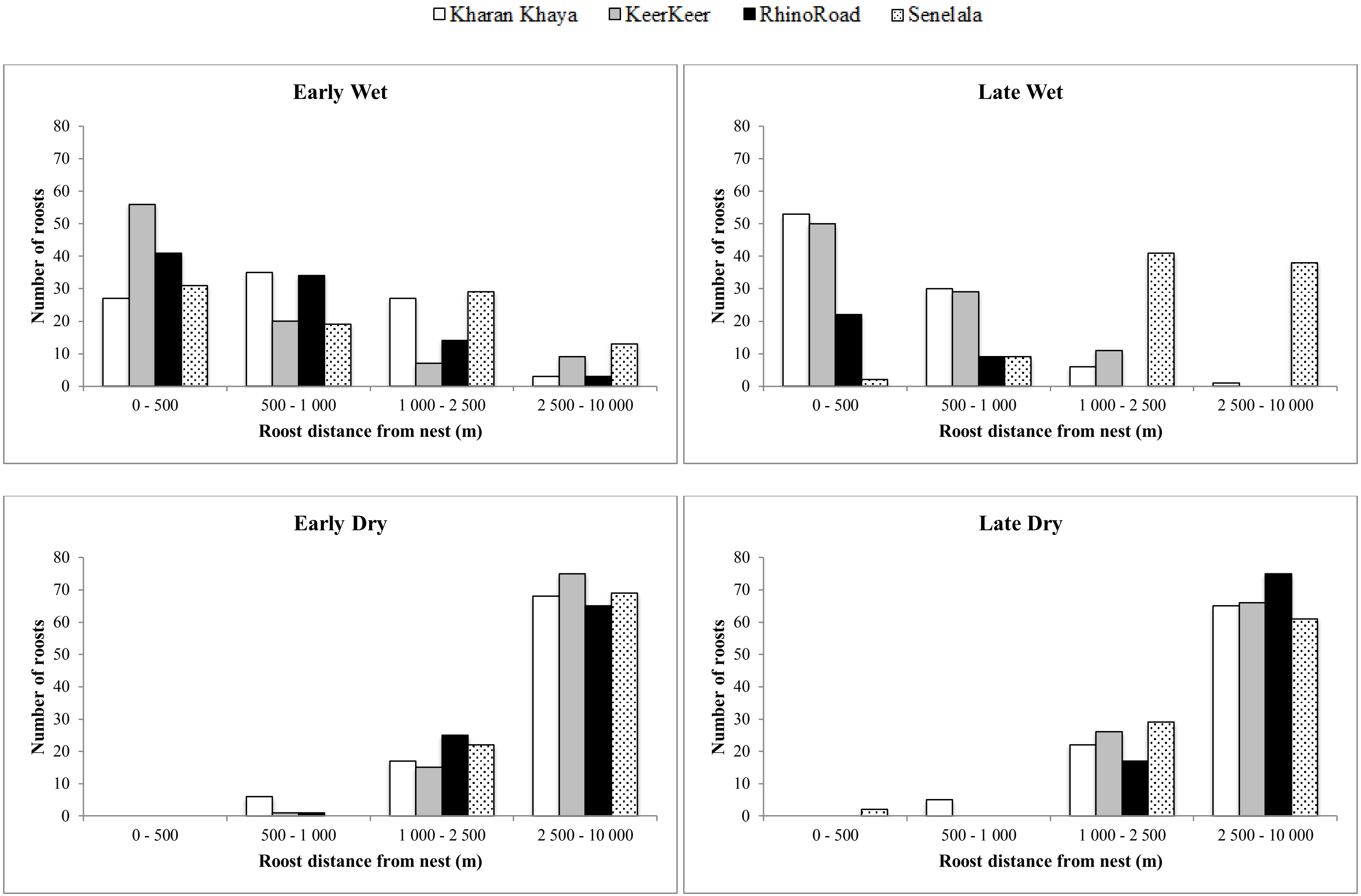


Figure 3.2: Mean distance between roost sites and the nest of four Southern Ground-Hornbill groups per season in the APNR, northeast South Africa.

Mean distance between nightly roost sites per season

The monthly mean distance between nightly roost sites of all four groups was lowest in the Early Wet season, with mean distances ranging from 691-1 238 m (Figure 3.3). In the Late Wet season, the three groups that bred successfully maintained a low mean distance between successive roosts (383-1 242 m, excluding the Rhino Road group, which lacked data for February and March), while the failed Senelala group displayed an increased distance between successive roost sites (1 809-2 876 m). Throughout the Early Dry and Late Dry seasons, all four groups displayed an increased mean distance between successive roost sites (1 987-3 789 m and 3 241-3 998 m respectively).

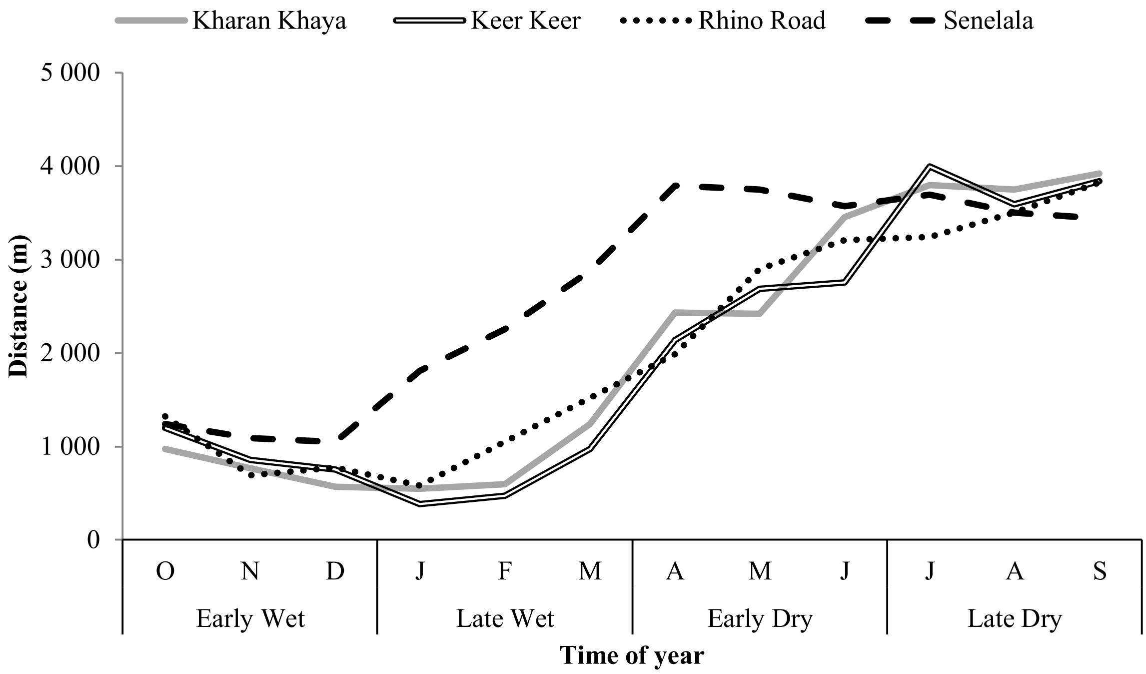


Figure 3.3: Monthly mean distance between nightly roost sites of four Southern Ground-Hornbill groups throughout the year in the APNR, northeast South Africa.

Habitats in which roosts occur

In the wet season, riparian habitats were favoured for roosting by the three groups that bred successfully, whereas the Senelala group (which failed) did not appear to favour any particular habitat type, and avoided riparian habitats (Table 3.4). In the dry season, the Kharan Khaya group switched to favouring disturbed areas and the Rhino Road group to combretum-dominated habitats, while Keer Keer and Senelala favoured mopane-dominated habitats.

Table 3.4: The degree of seasonal habitat selectivity for roosting by four Southern Ground-Hornbill groups in the APNR, northeast South Africa, where values range from +1 to -1, with values > +0.25 indicating preference, values < -0.25 indicating avoidance and values between +0.25 and -0.25 indicating neutral attraction.

Habitats	Kharan Khaya		Keer Keer		Rhino Road		Senelala	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Acacia	-0.20	-0.07	0.01	-0.07	-0.26	-0.29	0.13	-0.04
Combretum	-0.53	-0.11	0.06	0.03	-0.07	0.29	-0.11	-0.11
Mopane	-0.15	-0.06	-1.00	0.41	0.08	0.22	0.13	0.26
Riparian	0.64	0.28	0.38	-0.38	0.60	0.13	-0.71	-0.85
Terminalia	-	-	-	-	-0.73	-0.21	-	-
Disturbed	0.38	0.68	-1.00	-1.00	-	-	-1.00	-1.00

Discussion

Ground-hornbills are not known to make use of regular roost sites (Kemp, 1995), so we might expect to find a low frequency of repeated roost site use and a large number of individual roost sites utilised, as was the case for all groups throughout the non-breeding season, and breeding groups after their breeding attempt failed. During the summer breeding season, groups that bred successfully displayed a higher frequency of roost site use and therefore a smaller number of individual roost sites utilised, reflecting a degree of seasonal roost site loyalty. However, they always used at least 5-10 roost sites per month, suggesting that breeding roost sites probably represent a trade-off between the convenience of being close to the nest and the need to avoid being too predictable to potential predators (Kemp, 1995). This was confirmed by the lowest mean distances between roost sites and the nest and between nightly roost sites being strongly related to breeding activity and breeding success, with groups concentrating roosting close to the nest throughout the breeding season. Proximity of roost sites to the nest peaked as the breeding season progressed, coupled with a decrease in the mean distance between nightly roosts. This has been recorded in other hornbills (Bucerotidae), where the breeding female is restricted to roosting in the sealed nest while the breeding male and other group members roost nearby (Kemp, 1995). Once a breeding attempt fails, the group is free to roam more widely (Chapter 2) and the group no longer roosts near the nest.

Breeding groups favoured roosting sites in riparian habitats. Ground-hornbills nest in natural cavities in large trees such as *Ficus sycomorus*, *Diospyros mespiliformis* and *Combretum* *imberbe*, which in drier habitats such as the APNR generally occur along watercourses (Kemp & Kemp, 1980; Kemp & Begg, 1996; Msimanga, 2004; Jordan, 2011). This explains why riparian habitats were (1) favoured during the wet season, when breeding groups roosted in close proximity to the nest, (2) why unlike the three successful breeding groups, the Senelala group did not favour riparian habitats, as once their chick had died, the group was no longer constrained to habitats around the nest, and (3) why riparian habitats were not favoured during the dry season, as groups moved around in search of food and could simply roost where they ended their day's foraging.

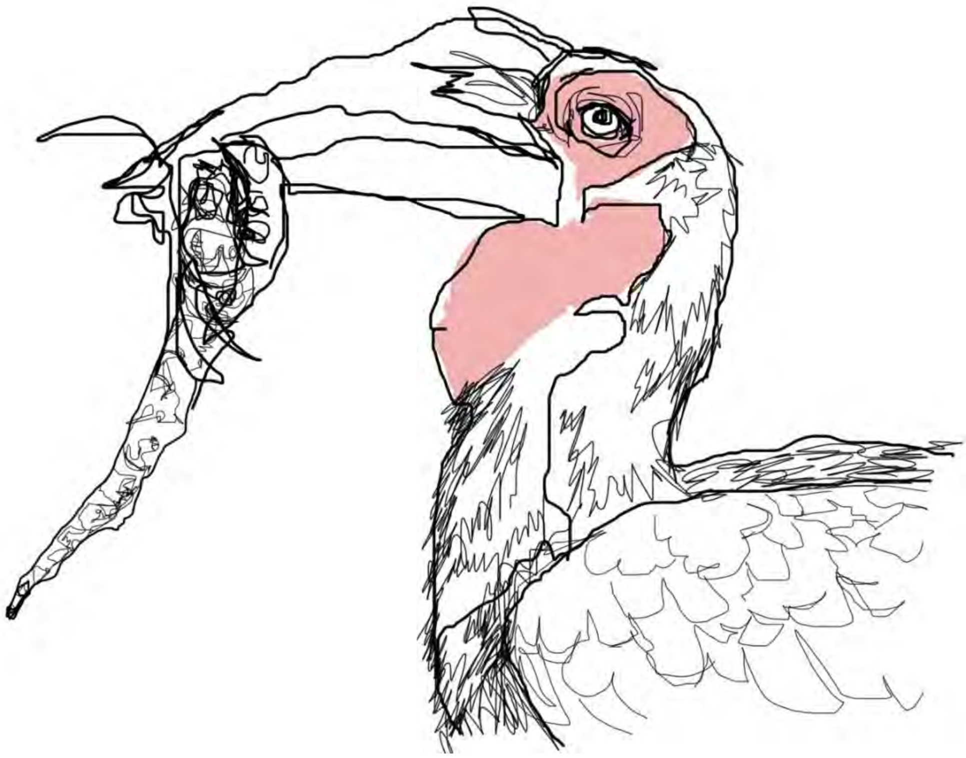
The importance of large trees, with a diameter at breast-height of >1 m, which can have cavities with a minimum internal diameter of 40 cm for the availability of suitable nesting sites for Southern Ground-Hornbills in savannas is well known (Kemp *et al*, 1989; Kemp & Begg, 1996). This study confirms this, and stresses the importance of these large trees as well as habitats in close proximity to the nest for the rest of the breeding group for safe roosting, both along riparian strips during the breeding season and throughout the savannas for the rest of the year. Habitat management should therefore take cognisance of this when considering the structural composition of the savannas and the potential threats to current and future large trees which Southern Ground-Hornbills are known to use for nesting and roosting, specifically *Faidherbia albida*, *Ficus sycomorus* and *Diospyros mespiliformis* along water courses and *Adansonia digitata, Combretum imberbe* and *Sclerocarya birrea* away from drainage lines in these landscapes.

Appendices

Appendix 3.1: Monthly mean nautical dusk and mean nautical dawn times for the town of Hoedspruit, the closest weather station to the APNR (~20 km from the centre of the APNR).

Season	Month	Mean nautical dusk	Mean nautical dawn
Early Wet	October	18:44	04:47
	November	19:02	04:17
	December	19:26	04:03
Late Wet	January	19:43	04:14
	February	19:38	04:40
	March	19:15	05:00
Early Dry	April	18:44	05:15
	May	18:19	05:26
	June	18:08	05:39
Late Dry	July	18:12	05:47
	August	18:23	05:41
	September	18:23	05:18

SYTHESIS AND REFERENCES



Synthesis

The Southern Ground-Hornbill Species Recovery Plan for South Africa published in 2011 aims to halt the decline in numbers and range contraction and to affect an increase in the population size and area of occurrence within the historic range of the species. The plan also highlights key gaps in the existing knowledge of the biology and ecology of the Southern Ground-Hornbill, of which, a greater understanding of the habitat requirements of the species is listed. Population-level threats to the species include habitat alteration mostly due to agricultural practices, particularly outside of protected areas, and probably even conservation practices in protected areas. This thesis aimed to fill some of these gaps and gain a better understanding of habitat suitability by looking at the fine-scale movements and habitat use of the Southern Ground-Hornbill in the Associated Private Nature Reserves, northeast South Africa.

I determined that Southern Ground-Hornbills display seasonal variations in movement distances, with groups travelling further during the summer breeding season than in the winter, despite smaller summer home ranges and the constraints of central place foraging. I also determined that temperature played a key role in movement distances as well as the type of habitat used. Furthermore, I determined that Southern Ground-Hornbills exhibit a degree of seasonal roost site loyalty and are more selective of roost sites than was previously thought.

These new insights into the fine-scale movements and habitat use of the species are of value when assessing habitat management options for the species, particularly with regards to the reintroduction of founder groups and the placement of artificial nests. Likewise, adequate large trees for nesting and roosting, particularly in riparian habitats, may be an important and potentially limiting factor for the successful reproduction of Southern Ground-Hornbills. In particular, this added knowledge should be integrated into landscape-level conservation planning for the enhancement of current and future habitat suitability for the species.

I therefore recommend that habitat management strategies and decisions should take cognisance of this when considering the botanical composition of the savannas and the potential threats to current and future large trees, particularly *Faidherbia albida*, *Ficus sycomorus* and *Diospyros mespiliformis* along water courses and *Adansonia digitata, Combretum imberbe* and *Sclerocarya birrea* away from drainage lines in these landscapes.

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